TEMPORAL VARIATION IN NATURAL AND SEXUAL SELECTION OF MALE CALLING BEHAVIOR IN THE FIELD CRICKET *GRYLLUS RUBENS*

By

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By

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A primary goal of sexual selection theory is to understand how natural and sexual selection interact to favor variation in sexually-selected traits. The goal of this dissertation is to examine variation in male calling behavior of the field cricket *Gryllus rubens* and how temporal changes in natural and sexual selection may favor this variation. The results of this dissertation are important because they show that temporal variation in natural and sexual selection may favor variation in male sexually-selected traits.

Male calling song in *G. rubens* attracts females. It also attracts gravid females of the parasitoid fly *Ormia ochracea*. These female flies deposit larvae on and around calling males, killing infected crickets within 7-10 days. In northern Florida, *O. ochracea* is abundant in the fall and rare in the spring, and fly parasitism rates are higher in the fall than in the spring. This temporal variation in natural selection could favor different male songs in the fall than in the spring. I

evaluated this possibility by examining seasonal variation in male calling behavior. I found that fewer males sing each night in the fall than in the spring and that fewer males sing at times when parasitoid flies are most active.

Because seasonal changes in parasitoid fly abundance may change the costs and benefit of choice, fall and spring females may behave differently towards calling males. I evaluated this hypothesis by observing the phonotactic behavior of fall and spring females. I found that fall females are less attracted to male songs than spring females at times when flies are most active.

Seasonal changes in sexual selection may change the seasonal benefits males derive from singing. I explored this hypothesis by examining whether the benefits of singing change seasonally and whether such changes are correlated with seasonal differences in male calling duration. The results of a playback experiment show that long duration calls attract more females in the fall, where call durations are long, than in the spring, where call durations are short.

Temporal changes in natural and sexual selection may favor seasonal variation in male *G. rubens* calling behavior. To evaluate how such fluctuating selection may affect seasonal patterns in calling duration, I developed a model evaluating the fitness of different calling strategies in the fall and spring given seasonal changes in natural and sexual selection. By varying these selective forces independently and comparing the fitness of calling strategies to observed calling durations, I found that temporal changes in sexual selection may have a greater effect on calling duration than changes in natural selection.

CHAPTER 1
GENERAL INTRODUCTION

A primary goal of sexual selection theory is to understand how natural and sexual selection interact to favor variation in male sexually-selected traits (Andersson 1994). Crickets are ideal subjects for the study of sexually selected traits for several reasons. First, males produce calling songs to attract females for mating, and females select mates based on the quality of their songs (for review see Loher & Dambach 1989). This means that male song is likely to be influenced by sexual selection. Second, many song characters are highly variable among males (Cade & Wyatt 1984, Cade 1991, Walker 1998, 2000). Third, song characters can be manipulated independently from male phenotype by tape recording male calling songs and editing the recordings. This provides a means of isolating different song characters and testing for their separate effects on female choice (Hedrick 1986). Fourth, females choose males overtly: they approach males and mount them. This female behavior offers the opportunity to separate the effects of female choice from male-male competition. Additionally, because females approach speakers broadcasting male songs in the same way they would approach calling males, female choice can be studied without the problem of males adjusting their song in response to females, and females modifying their preference in response to changes in male song. Collectively, these characteristics make crickets model subjects for studies on sexual

selection (Cade 1979, Crankshaw 1979, Boake 1984, Hedrick 1986 & 1988, Simmons 1988).

The goal of this dissertation is to examine variation in male calling behavior of the field cricket *Gryllus rubens* and how temporal changes in natural and sexual selection may favor this variation. The results of this dissertation are important because they show that temporal variation in natural and sexual selection may favor variation in male sexually-selected traits.

The field cricket *G. rubens* is well suited for studying the effects of natural selection on calling song traits. In addition to attracting females, the calling song of male *G. rubens* also attracts gravid females of the parasitoid fly *Ormia ochracea* (Walker 1986, 1993). These female flies deposit larvae on and around calling males, killing infected crickets within 7-10 days. In northern Florida, *O. ochracea* is abundant in the fall and rare in the spring (Walker 1986), and fly parasitism rates are higher in the fall than in the spring (Walker & Wineriter 1991). This seasonal variation in the costs of calling suggests that natural selection on male calling song varies temporally. This temporal variation in natural selection can result in different calling songs in different seasons. I examine this hypothesis in the second chapter of this dissertation by exploring whether male *G. rubens* exhibit seasonal variation in calling behavior and whether this variation is associated with seasonal changes in parasitoid fly abundance.

Gryllus rubens is also well suited for studying the effects of temporal variation in sexual selection. Even though females do not sing, Walker and

Wineriter (1991) have shown that females can also be parasitized. If females are infected as they approach calling males, then the costs of mate choice may be higher in the fall when flies are abundant than in the spring when flies are rare. These seasonal changes in the costs of mate choice may cause females to be less attracted to male calling song in the fall than in the spring to reduce the risk of fly parasitism. This temporal variation in female behavior may alter the strength of sexual selection seasonally. I evaluate this hypothesis in the third chapter of this dissertation by examining female attraction to male calling song at different times of the year.

Seasonal variation in sexual selection may alter the seasonal benefits that males derive from singing. As a result, such variation may favor seasonal changes in male calling behavior. I evaluate this hypothesis in the fourth chapter of this dissertation by examining whether the benefits of singing change seasonally and whether such changes are correlated with seasonal differences in male calling duration.

I conclude this dissertation with a discussion of how temporal changes in natural and sexual selection should affect seasonal variation in male *G. rubens* calling duration. I test these effects by calculating the fitness of different calling strategies in the fall and spring given seasonal changes in natural and sexual selection. By varying natural and sexual selection independently, I estimate the relative importance of natural versus sexual selection in favoring variation in male calling duration.

By studying male calling behavior and the benefits that males derive from singing when flies are rare and abundant, this dissertation examines how temporal variation in natural and sexual selection may interact to favor variation in male sexually-selected traits.

CHAPTER 2
VARIABLE SELECTION FOR MALE SONG IN THE FIELD CRICKET *GRYLLUS RUBENS*

Introduction

Conspicuous male traits such as bright colors, large size, or elaborate behavior evolve through the joint action of sexual and natural selection (Andersson 1994). Sexual selection favors males with conspicuous traits since these traits are advantageous in mate acquisition through either female choice or male-male competition (Darwin 1871). Natural selection, on the other hand, acts against males with conspicuous traits if these traits lower male survival. Conspicuous traits may lower survival by being energetically costly or by making males more vulnerable to predators. Therefore, conspicuous male traits evolve depending on the relative strength of sexual and natural selection. This hypothesis predicts that when the costs of natural selection increase relative to the benefits of sexual selection, then males should become less conspicuous. In this study, I evaluate this prediction by examining the male calling behavior of the field cricket *Gryllus rubens* in two seasons that differ in the risk of parasitism from acoustically orienting flies.

Male crickets produce calling songs by rubbing their raised forewings together, which attracts conspecific females for mating (Loher & Dambach 1989). In some species, the same calling song also attracts parasitoid flies which deposit larvae on and around calling males, killing infected crickets within 7-10

days (Cade 1975, Walker 1986, 1993). This fly parasitism risk has been used to explain variation between species in the nightly calling duration of male field crickets (Orthoptera; Gryllidae). Cade and Wyatt (1984) found that male *G. texensis*, which is parasitized, spend less time calling per night than male *G. veletis*, *G. pennsylvanicus*, and *Teleogryllus africanus,* which are not parasitized by phonotactic flies. They argue that fly parasitism has selected against long nightly calling in species that are parasitized. They also found that the distribution of male *G. texensis* nightly calling duration is highly skewed because some males do not call. It is thought that males that do not call or males that sing less search for females so there is some expectation of success for these males, particularly when female densities are high. Cade and Wyatt (1984) attribute the skew distribution of nightly calling duration in *G. texensis* to the higher rates of parasitism in this species.

However, species differences in time spent calling per night may be due to species differences in the energetic costs of singing. The song of *G. texensis* is made up of sound pulses organized into trills. In contrast, the songs of *G. veletis* and *G. pennsylvanicus* are composed of sound pulses grouped into chirps with quiet periods between them. Because trilling songs may be more energetically costly than chirping songs (Prestwich & Walker 1981, Prestwich 1994), differences in time spent calling per night between the trilling *G. texensis* and the chirping *G. veletis* and *G. pennsylvanicus* may be explained by energetic differences in song production. Collectively, these findings cannot separate the

effects of fly parasitism risk and energetic costs of calling on nightly calling duration in male crickets.

Fly parasitism risk has also been used to explain variation in the timing of male calling in crickets. French and Cade (1987) found that male *G. texensis* call more around dawn than in the early evening. They hypothesized that dawn calling is common in *G. texensis* because parasitoid flies are less active at dawn. However, *G. veletis* and *G. pennsylvanicus* also call more around dawn (French & Cade 1987), and they are not infected by parasitoid flies. Furthermore, in all three species, male calling around dawn coincided with increased female movement and mating activities (French & Cade 1987). Therefore, it is not clear whether male *G. texensis* call more around dawn because flies are less active at that time or because females are more sexually receptive around dawn.

Testing the effect of fly parasitism risk on nightly calling duration and timing of calling in male crickets under laboratory conditions is difficult because it is possible that crickets do not respond directly to flies but rather to environmental cues associated with fly activity. If so, then examining male calling behavior in an experimental arena with and without flies will not reveal the effect of parasitoid flies on behavior. One solution to this problem is to study male calling behavior in populations with and without parasitoid flies. This is the approach that was used by Zuk et al. (1993) and Simmons et al. (2001). However, any correlation between male calling behavior and fly abundance may also be explained by environmental or other differences between the two populations (for example, populations without flies may be at higher latitudes

than those with flies). This limitation of working with geographically distinct populations is overcome when studying a population that is exposed to seasonal changes in fly abundance. This is the case for the field cricket *G. rubens*. The calling song of this species attracts gravid females of the parasitoid fly *Ormia ochracea* (Walker 1986, 1993). In northern Florida, *O. ochracea* is abundant in the fall and rare in the spring (Walker 1986), and fly parasitism rates are higher in the fall than in the spring (10% versus 0%; Walker & Wineriter 1991). These seasonal differences in fly abundance and rates of parasitism suggest that the costs of calling are higher in the fall than in the spring. This seasonal variation in natural selection serves as a natural experiment to examine the effect of fly parasitism risk on nightly calling duration, number of males calling and timing of calling in male crickets.

I hypothesize that seasonal changes in natural selection favor seasonal changes in male calling behavior in *G. rubens*. Accordingly, I made the following predictions. First, I predicted that fewer males would call in the fall than in the spring because some males do not sing (personal observation) and experimentally muted males have lower rates of fly parasitism than non-muted males under high fly densities (Walker & Wineriter 1991). Second, I expected that males should spend less time calling per night in the fall than in the spring because the number of parasitoid flies attracted to broadcasts of cricket songs increases with broadcast duration (Cade et al. 1996). Third, I expected that fewer males would call in the early evening in the fall than in the spring because parasitoid fly activity is highest in the early evening (Cade et al. 1996). I tested

these predictions by recording the calling duration of individual males under field conditions and conducting nightly surveys of singing males.

Finding that variation in male calling behavior in *G. rubens* is correlated with seasonal changes in natural selection from the risk of fly parasitism would be important because it would help us understand how males deal with the conflicting demands of attracting females while avoiding parasitism. Because males of many animal species have mating signals that attract both females and predators and/or parasites (reviewed by Burk 1982 and Magnhagen 1991), the results of this study may have important implications for many systems in which males or females attract mates with conspicuous displays.

Methods

Study Species

The field cricket *Gryllus rubens* is found in lawns, pastures, and along roadsides in southeastern United States (Alexander 1957). Unlike most other species of field crickets, male *G. rubens* produce a trilling song in which sound pulses are repeated and grouped into long pulse trains (Doherty & Callos 1991). This trilling song attracts females who approach and mount males. It also attracts gravid females of the parasitoid fly *Ormia ochracea* (Walker 1986, 1993).

Fly Abundance and Activity

To confirm that *O. ochracea* flies are more abundant in the fall than in the spring and that flies are most active in the early evening, I monitored nocturnal changes in fly activity in a pasture at the University of Florida Beef Teaching Unit, Alachua Co., FL that was 1-km from the transects used in the night surveys. To monitor fly activity, I used a slit trap (Walker 1989) with an electronic sound synthesizer that broadcasts calls of *G. rubens* (4763 Hz carrier frequency, 50.0 pulses per second, 50% duty cycle; continuous trill at 106 dB, 15 cm above the speaker). I activated the synthesizer an hour before sunset and counted the number of flies captured at the trap 3, 7, 11, and 13 h after sunset. I carried out this procedure in the fall from 20 September to 17 November 2000 (N=8) and spring from 3 April to 23 May 2001 (N=6).

Field Recordings of Individual Males

To study seasonal changes in the number of calling males and time spent calling by males per night, I recorded the calling duration of individual males under field conditions. For these recordings, I collected adult males from a field at the University of Florida Environmental Landscape Horticulture Education Lab, Alachua Co., FL, using a sound trap with an electronic sound synthesizer (Walker 1986). Males were weighed to the nearest 0.001 g and placed individually in square plastic containers measuring 13 x 13 x 9 cm (l x w x h) with wire screen lids for 10 days to ascertain that they were not parasitized by *O. ochracea*. Each container had an inch of sand, an inverted egg carton shelter,

and Purina Cat Chow and water ad lib. All crickets were held under ambient light and temperature in a greenhouse less than 1 km from the collection site. After 10 days, I transferred the containers to the field and laid them out in a straight line keeping a distance of 15 m between containers. This distance was chosen so that males could not hear the singing of other males being recorded. Each plastic container was set in a square aluminum pan measuring 20 x 20 x 4 cm (l x w x h) with an inch of water to prevent fire ants from invading the containers. Next to each container, I placed an Optimus model CTR-115 voice-activated cassette tape recorder. I switched on all tape recorders an hour before sunset and allowed them to run for 16 h. All tape recorders were checked hourly to replace any tapes that were full. Two to four males were recorded each night. I electronically monitored 20 males over nine nights in the spring (April/May 2001) and 23 males over nine nights in the fall (September/October 2001). Each male was monitored only once. Fall and spring field recordings did not differ in the minimum temperature recorded each night ($Mean_{fall} \pm SE = 15.44 \pm 1.35$ °C, $Mean_{spring} \pm SE = 15.59 \pm 1.64$ °C, $P=0.943$). There was also no seasonal difference in the maximum temperature recorded each night ($Mean_{fall} \pm SE = 30.06 \pm 0.86$ °C, $Mean_{spring} \pm SE = 28.16 \pm 1.37$ °C, $P=0.260$).

I calculated the nightly calling duration for each male by listening to the tapes with a stopwatch. If the male stopped calling for more than 2 sec, then the stopwatch was stopped until the male resumed calling. The nightly calling duration was the total time spent calling during the 16 h that males were monitored.

Night Surveys

I studied seasonal changes in the number of calling males and the timing of calling by conducting night surveys of singing males in a pasture used to graze cows at the University of Florida Beef Teaching Unit. This pasture was divided into 10 130 x 20 (l x w) m parallel transects. A night survey consisted of a 16 h sampling period beginning an hour before sunset in which I walked in a straight line through the center of each of five transects randomly selected at 4 h intervals counting the number of calling males. At the start of each 4 h interval, I recorded the temperature in each transect 2 cm above the soil. On a given night, the same five transects were surveyed four times during the 16 h survey period. Each transect was surveyed two to three nights each season. Fall surveys were conducted from 23 September to 17 November 2000 and spring surveys from 3 April to 23 May 2001 because these are the dates when flies were shown to be abundant and rare, respectively (Walker 1986).

To test the prediction that fewer males will call in the early evening in the fall than in the spring, I performed a Repeated Measures ANOVA on the number of calling males in the night surveys. This variable was transformed to achieve normality by adding 0.375 to the variable and taking the square root of this sum (Ott 1993). This transformation achieved normality and validated the sphericity assumption (variance-covariance matrix of dependent variable is circular in form) of the Repeated Measures ANOVA. The terms season (fall and spring) and time (4 h interval) were used as factors. The average temperature across the four time intervals in each transect was used as a covariate. Only one night survey per

transect was used in this analysis. For each transect, I chose the first night survey where the average temperature recorded in the four time intervals fell between 15 and 25 °C. This restriction was used to limit the effect of extreme temperatures on male calling behavior. For this analysis, I assumed that transects were independent between seasons because the lifespan of males is likely to be shorter than the time elapsed between the fall and spring night surveys.

Data were analyzed using SYSTAT 6.0 and SPSS 11.5. Results are presented as means ± standard error.

Results

Fly Abundance and Activity

Ormia ochracea flies were much more common in the fall than the spring. In the fall, a mean (±SE) of 17.6 ± 6.2 flies/ night were captured at the slit trap (N=8). In contrast, no flies were ever captured in the spring (N=6). In the fall, the number of *O. ochracea* flies captured was highest in the first few hours after sunset (Fig. 2-1). Flight activity then steadily declined throughout the remainder of the night but showed a small increase around dawn (i.e., 13 hours after sunset).

Field Recordings

A higher proportion of males sang in the spring, 15/20 (75%), than in the fall, 10/23 (43%) (Fisher's exact test: P=0.030). Overall, fall males did not differ in nightly calling duration (44.5 min ±13.8) from spring males (31.8 min ±9.1) (t-test, N_{fall}=23, N_{spring}=20, t=0.765, P=0.449). However, when males that did not sing at any time during the 16 h test period were excluded from this analysis, then fall males that sang spent more time calling (102.3 min ± 20.3) than spring males that sang (42.4 min ± 10.9) (Fig. 2-2; t-test, N_{fall}=10, N_{spring}=15, t=2.60, P=0.020). Although fall males were heavier than spring males (Fig. 2-3; t-test, N_{fall}=23, N_{spring}=20, t=3.693, P=0.001), male mass did not have a significant effect on nightly calling duration for males that sang in either the fall (Fig. 2-4; N=10, R^2=0.090, P=0.399) or the spring (Fig. 2-4; N=15, R^2=0.002, P=0.885).

Night Surveys

More males were observed singing in the spring than in the fall across all sampling periods in all surveys (Fig. 2-5; Repeated Measures ANOVA, season, $F_{1,18}$=8.769, P=0.008). Time of day had a significant effect on the number of calling males (Fig. 2-6; Repeated Measures ANOVA, 4 h interval, $F_{3,54}$=7.319, P<0.001). More males sang in the first few hours after sunset in the spring than in the fall (Fig. 2-6; Repeated Measures ANOVA, time*season, $F_{3,54}$=3.776, P=0.016). These results came from a model that excluded temperature as a covariate. Temperature was excluded because a preliminary model with season

and time as factors and temperature as a covariate showed that temperature did not have a significant effect on the number of calling males (Repeated Measures ANOVA, temperature, $F_{1,17}=0.058$, $P=0.812$).

Discussion

This study has shown that seasonal changes in male *G. rubens* calling behavior are correlated with seasonal changes in the risk of fly parasitism. The probability of encountering parasitoid flies on a given night is higher in the fall than in the spring. In the fall, this probability is highest in the early evening and then declines steadily throughout the night. This suggests that the natural selection costs of calling per night are higher in the fall than in the spring, and that these costs decrease within a night in the fall. As predicted by these seasonal changes in the risk of fly parasitism, a lower proportion of males sang in the fall than in the spring and fewer males sang in the early evening in the fall than in the spring. These findings are consistent with the hypothesis that natural selection affects the evolution of sexually selected male traits. When the natural selection costs of conspicuous traits increase relative to the benefits, then males behave less conspicuously.

However, other factors besides the risk of fly parasitism change seasonally and may explain the seasonal variation in the number of calling males. These factors include differences in density, differences in the proportion of parasitized males, and differences in male size between seasons. Differences between seasons in female behavior will be discussed in chapter 3. Fewer

males may have sung in the fall than in the spring because fewer males were present. Several lines of evidence argue against this possibility. First, Veazey et al. (1976) found that *G. rubens* densities in northern Florida are higher in the fall than in the spring. Second, my field recordings of individual males showed that a smaller proportion of males sang in the fall than in the spring. Alternatively, fewer males may have sung in the fall than in the spring because a higher proportion of males were parasitized. Parasites have been shown to decrease the ability of males to sing (Cade 1984, Kolluru et al. 2002). However, my field recordings show that this cannot entirely explain the pattern because healthy fall and spring males differed in calling behavior. Finally, fewer males may have sung in the fall than in the spring because spring males were larger than fall males. This is possible because male size has been shown to be correlated with calling duration in sagebrush and ground crickets (Sakaluk & Snedden 1990, Forrest et al. 1991). However, this cannot be an explanation for the seasonal differences in the number of calling males because fall males were heavier than spring males. The combined evidence suggests that fewer males sang in the fall than in the spring because the risk of fly parasitism is higher in the fall than in the spring.

More than half of the males that were recorded in the fall did not sing over the 16 h period they were monitored. If females approach calling males, how do these silent males get mated? It is likely that these males walk or fly around searching for females. This mating strategy has been described in several species of field crickets (French & Cade 1989, Hissmann 1990, Zuk et al. 1993, Hack 1998). Cade (1979) proposed that searching may be an alternative mating

tactic. He hypothesized that males using this tactic may have lower mating success on any given day than calling males. However, because searching males may also have lower rates of fly parasitism, they may have higher survival and longer lifespans than calling males. This type of alternative mating tactic has been described for guppies. Males usually display their bright color patterns to females by performing sigmoid displays in which males quiver their bodies in an S-shape (Baerends et al. 1955). Some males, however, do not perform these displays and instead attempt a sneak copulation by performing a gonopodial thrust. This mating tactic may be favored by natural selection because it is less conspicuous to predators than sigmoid displays (Endler 1987). This hypothesis has been supported by studies showing that males switch from sigmoid displays to gonopodial thrusts when the risk of predation is high (Endler 1987, Magurran & Seghers 1990, Reynolds et al. 1993, Godin 1995). Taken together, studies on crickets and guppies suggest that when the natural selection costs of conspicuous male traits increase, males may use alternative mating tactics. Males using these tactics are favored because even though they may have reduced mating success, they may have higher survival when compared to males using the more conspicuous tactic. Additionally, the success of searching males may increase as density increases.

As predicted, I found that more male *G. rubens* sang in the early evening in the spring than in the fall when flies were more active. French and Cade (1987) studied the timing of male calling in *G. texensis*, *G. veletis*, and *G. pennsylvanicus*. Their results showed that male calling increased at dawn in field

populations of all three species. Male *G. rubens* in this study did not increase calling around dawn. One possible explanation for this finding is that the small surge of parasitoid flies around dawn at my study site may have increased the natural selection costs of calling at those times. Consistent with this interpretation is the fact that the populations of *G. texensis* that French and Cade (1987) studied did not experience a surge in fly activity around dawn, and the populations of *G. veletis* and *G. pennsylvanicus* were not parasitized by *O. ochracea* (Cade & Wyatt 1984). Collectively, these studies suggest that the timing of male calling in crickets has responded to natural selection from parasitoid flies.

I predicted that males should spend less time calling per night in the fall than in the spring because the number of parasitoid flies attracted to broadcasts of cricket songs increased with broadcast duration (this study, Cade et al. 1996). The field recordings of individual males found the opposite result: fall males that sang spent more time calling per night than spring males that sang. Bertram (2002) also found the same seasonal pattern in male *G. texensis*. One factor that may explain these results is density. As density increases, males are expected to call less and search more because the gains from searching increase (Alexander 1961 & 1975, Otte 1977, Cade 1979). This effect has been demonstrated in experimental studies by showing that male calling decreases with density (Cade & Wyatt 1984, Cade & Cade 1992). However, seasonal differences in density cannot explain the seasonal differences in nightly calling duration from this study

nor the Bertram (2002) study because cricket densities at both sites were higher in the fall than in the spring (Veazey et al. 1976, Bertram 2002).

One possible explanation for the seasonal differences in nightly calling duration in *G. rubens* and *G. texensis* is sexual selection. If sexual selection for nightly calling duration is stronger in the fall than in the spring, then this seasonal difference in mating benefit may explain why fall males that sang spent more time calling than spring males that sang. I evaluate this hypothesis in chapter 4.

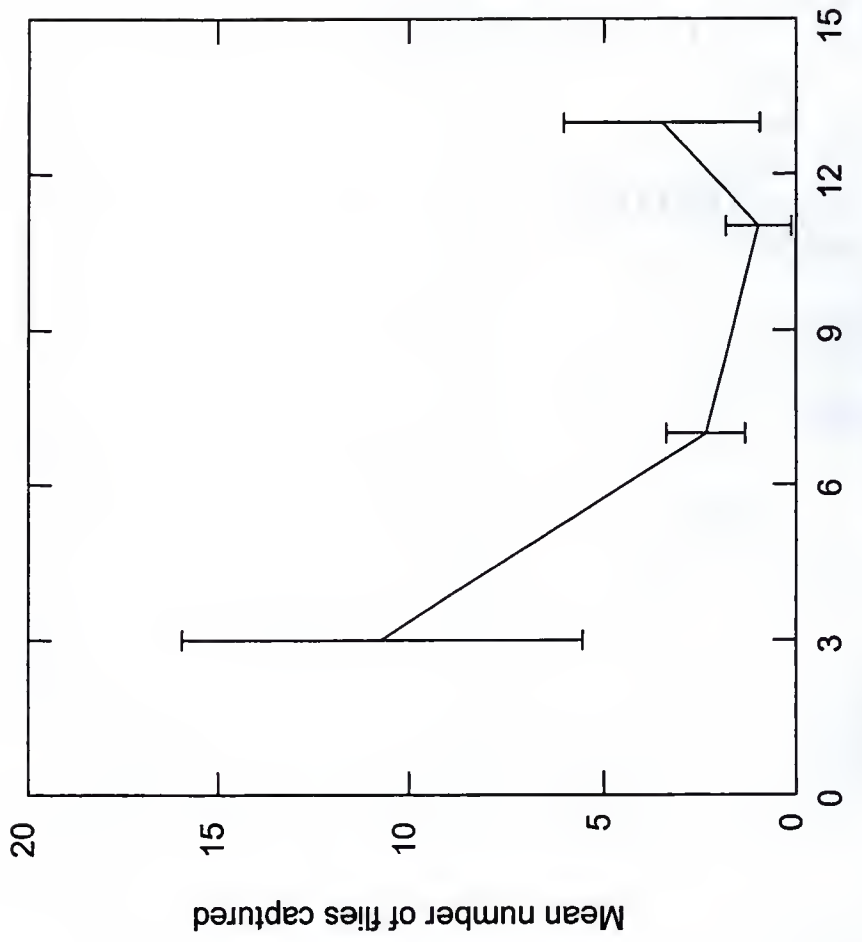

Fig. 2-1. Nocturnal changes in the mean number of *Ormia ochracea* flies captured at a slit trap broadcasting *Gryllus rubens* male calls over eight nights in the fall.

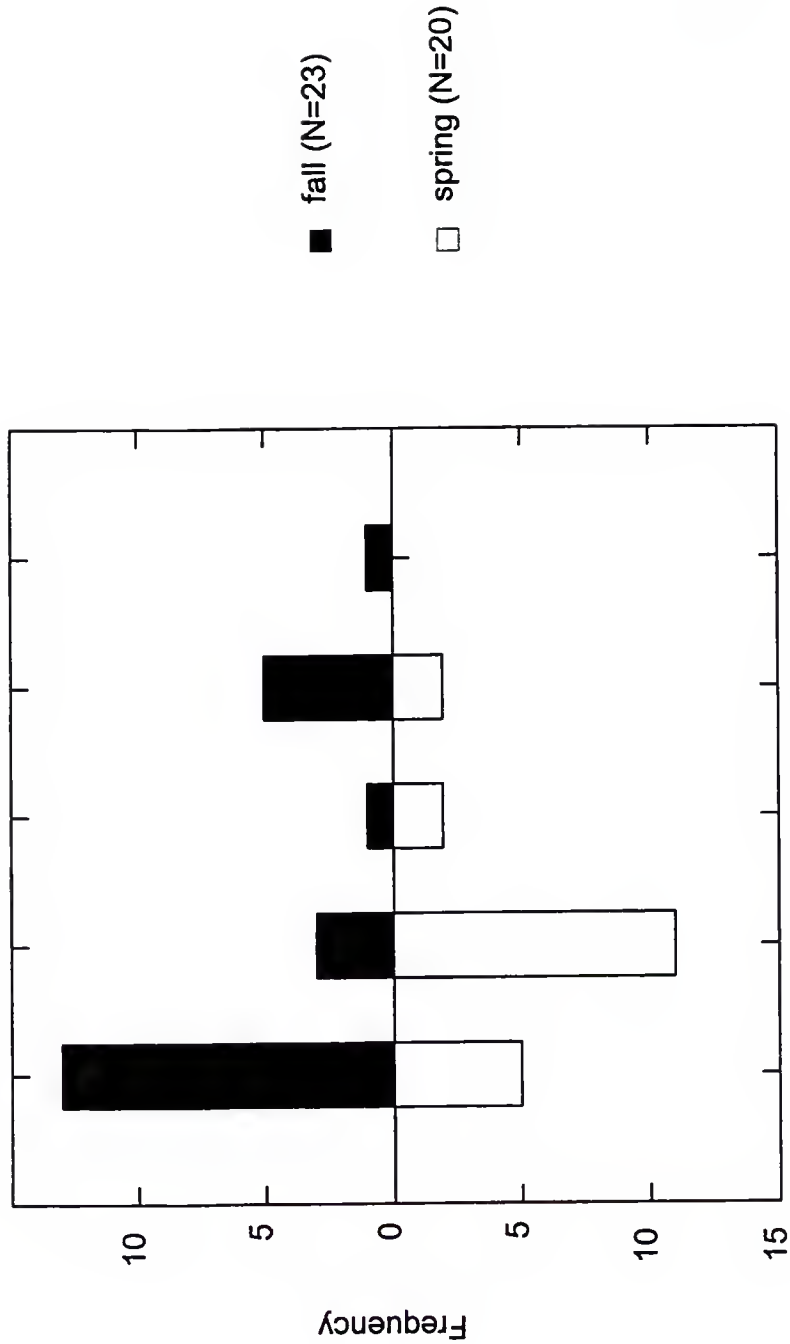

Fig. 2-2. Seasonal changes in the nightly calling duration of male *Gryllus rubens* individually recorded in the field during the fall and spring.

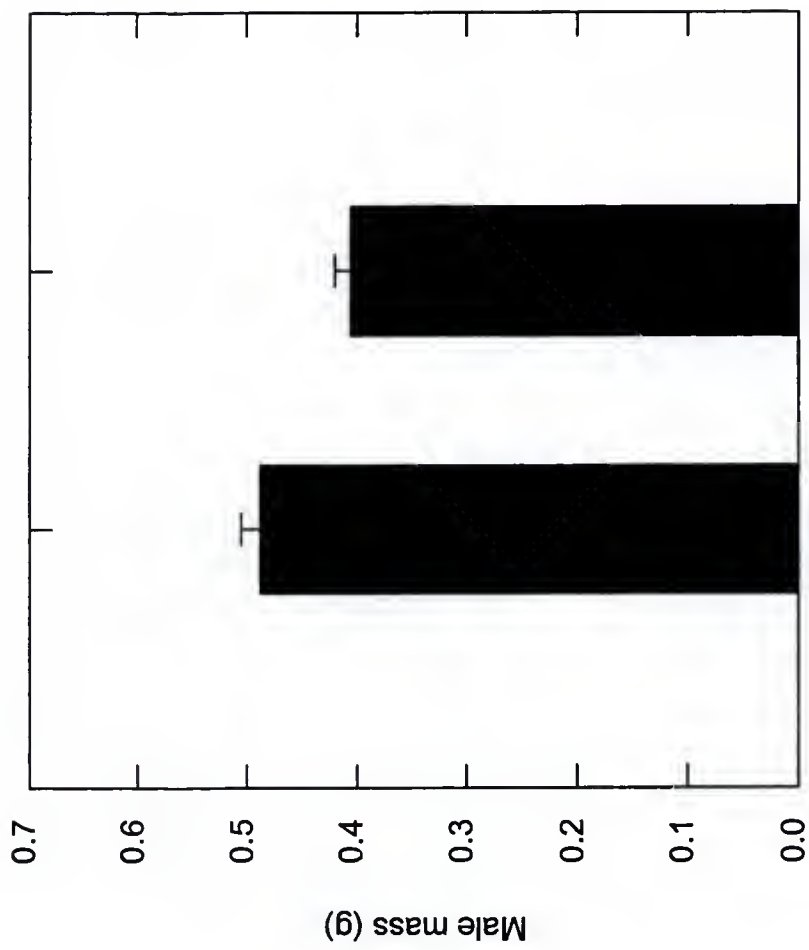

Fig. 2-3. Seasonal changes in male *Gryllus rubens* mass. Males were collected in the fall (N=23) and spring (N=20) using a sound trap. Each male was weighed to the nearest 0.001 g.

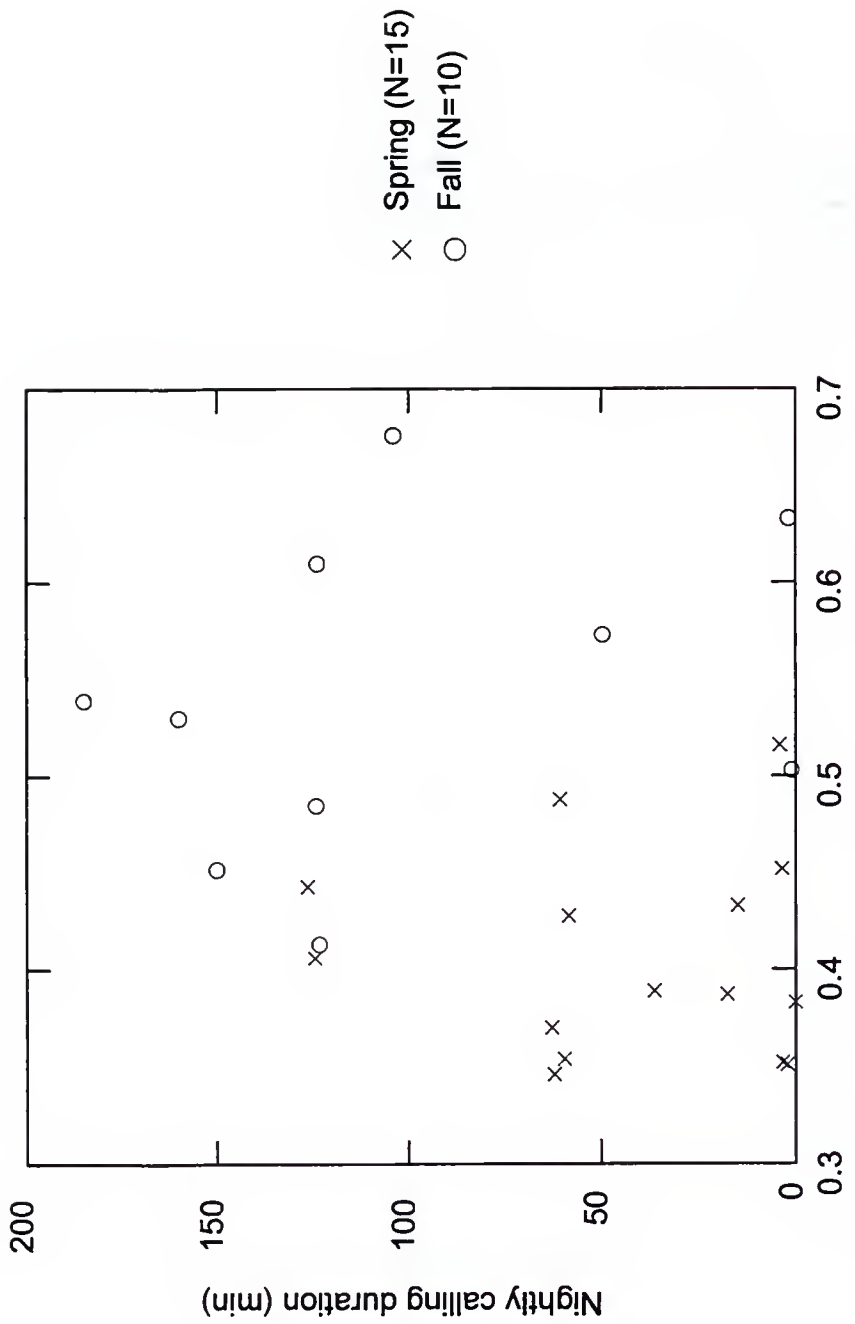

Fig. 2-4. Effect of mass on nightly calling duration of male *Gryllus rubens* individually recorded in the field during the fall and spring.

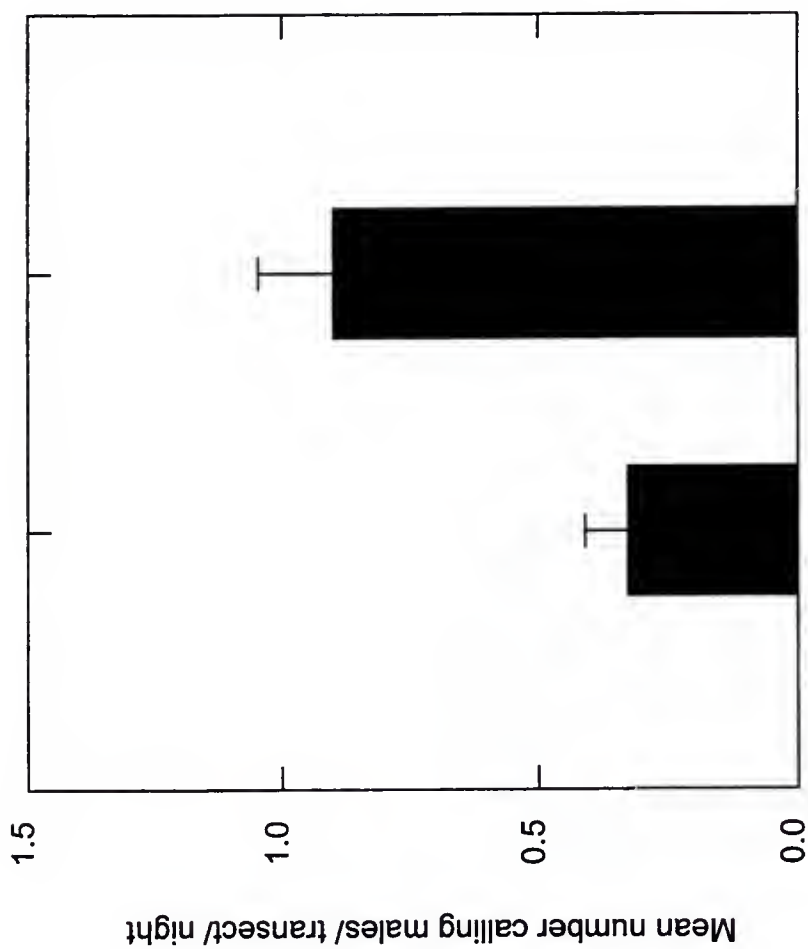

Fig. 2-5. Seasonal changes in the mean number of calling male *Gryllus rubens* over the night in surveys of 10 transects sampled in the fall and spring.

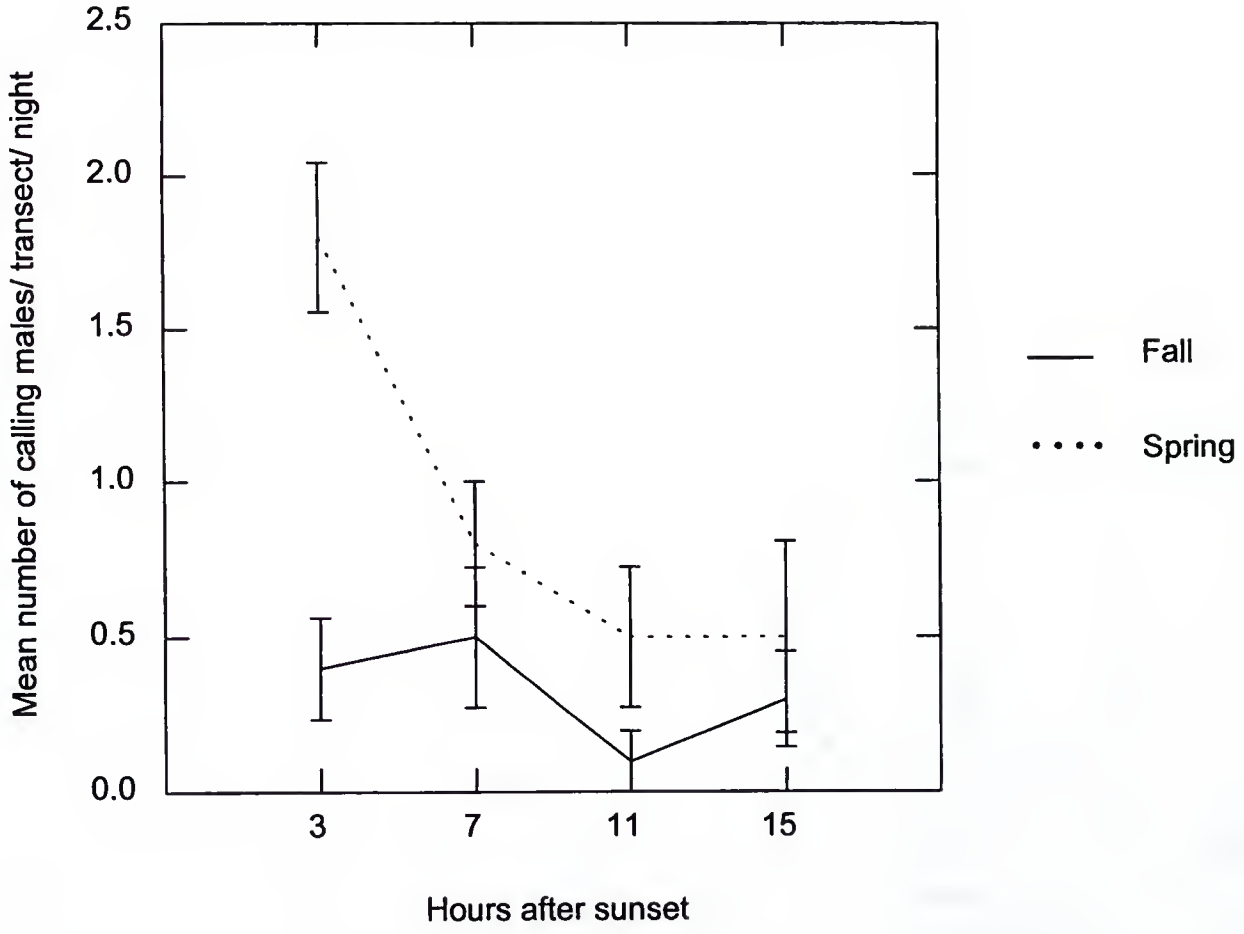

Fig. 2-6. Seasonal changes in the timing of male *Gryllus rubens* calling over the night in surveys of 10 transects sampled in the fall and spring.

CHAPTER 3
SEASONAL VARIATION IN FEMALE PHONOTAXIS TO MALE CALLING SONG OF THE FIELD CRICKET *GRYLLUS RUBENS*

Introduction

Males with sexually-selected traits are often at higher risk from predators and parasites (reviewed by Burk 1982 and Magnhagen 1991) than those without. Understanding how these risks affect female choice is important because theoretical models on the evolution of female preferences show that choosiness decreases when the risks of choice increase relative to the benefits (Parker 1983, Kirkpatrick 1987, Pomiankowski 1987, Real 1990, Iwasa et al. 1991). This is because females that choose conspicuous males may also experience increased risk of predation or parasitism because of their association with these showy males. A decline in choosiness will reduce the strength of sexual selection on male traits, which will cause males to become less extravagant. Therefore, males with sexually selected traits evolve to be less conspicuous when predation or parasitism is high not only because less conspicuous males survive better, but also because the benefits of conspicuousness through female choice are reduced. Despite the potential importance of these risks to females, few studies have examined how predation risk affects female choice (although see Dill et al. 1999). Similarly, while many studies have investigated female choice for males differing in parasitism levels (Borgia & Collis 1989, Hoglund et al. 1992, Houde & Torio 1992, Fitzgerald et al. 1994, Buchholz 1995, Kraaijeveld et al. 1997, Lopez

1998), no study has evaluated how parasitism risk affects female choice. In this study, I hypothesize that risk of parasitism decreases female attraction to males with sexually-selected traits. I evaluated this hypothesis by examining female phonotaxis to male calling song in the field cricket *Gryllus rubens* in two seasons that differed in the risk of parasitism from acoustically orienting flies.

Female *G. rubens* approach calling males and mount them for mating. The same male vocalizations that attract female crickets also attract gravid females of the parasitoid fly *Ormia ochracea*. Female flies deposit larvae on and around calling males, killing infected crickets within 7-10 days (Walker 1986, 1993). Even though females do not sing, Walker and Wineriter (1991) collected females during the fall of 1990 and found 10% parasitism (3 of 10) and a similar rate, 9%, among males (1 of 11). It is likely that females acquire parasites by interacting with calling males that have been attacked by *O. ochracea* that same night. Several lines of evidence support this idea. First, Walker and Wineriter (1991) experimentally muted males and found that unmuted males under high fly densities were not parasitized by *O. ochracea* (0 of 10) whereas non-muted males were (7 of 13). This suggests that calling is associated with fly parasitism. Because females do not sing and males only sing calling songs to attract females for mating (Loher & Dambach 1989), females are likely to be parasitized as they approach calling males. Second, *O. ochracea* flies deposit larvae around calling males. Females may become parasitized by walking over these larvae which adhere to them (Cade 1975, 1979, 1984). These scattered larvae may also explain how male and female *G. firmus* are parasitized by *O. ochracea* (Walker &

Wineriter 1991); *G. firmus* co-occur with *G. rubens* but their calls do not attract parasitoid flies (Walker 1986). This apparent link between female searching behavior and fly parasitism make *G. rubens* an ideal species to test the hypothesis that risk decreases female attraction to males with sexually-selected traits.

Parasitoid flies may decrease female *G. rubens* attraction to male calling song to minimize the risks of choice. In northern Florida, *O. ochracea* is abundant in the fall and rare in the spring (Walker 1986, Chapter 2), and fly parasitism rates are higher in the fall than in the spring (10% versus 0%, Walker & Wineriter 1991; chapter 2). This seasonality in fly abundance and parasitism rates suggests that fall females may incur higher risks of choice than spring females. Such costs may be greatest in the early evening because *O. ochracea* flight activity is highest just around dusk and then steadily declines (Cade et al. 1996, Chapter 2). These nocturnal changes in parasitoid fly activity may favor females that are less phonotactic to male calls in the early evening. This would be consistent with laboratory experiments on gobiid fish, crickets, and guppies, which have shown that female choosiness decreases when predation risk increases (Forsgren 1992, Hedrick & Dill 1993, Godin & Briggs 1996). Because *O. ochracea* flies are only active after dusk in the fall and not the spring (Chapter 2), I hypothesized that fall females would be less phonotactic to male calling song in the early evening than spring females. I evaluated this hypothesis by conducting a phonotactic experiment on fall and spring females shortly after dusk. In this experiment, females were given a choice between a silent speaker

and a speaker broadcasting male calls. I predicted that fewer females would choose the broadcasting speaker in the fall than in the spring, and fall females would spend less time near the broadcasting speaker than spring females. The potential finding that fall females are less attracted to male calling song in the early evening than spring females would be important because it would reduce the strength of sexual selection on males in the fall and help explain why fewer males sing around dusk in the fall than in the spring (Chapter 2).

Methods

Phonotactic Experiment

In this experiment, I quantified and compared among seasons the phonotactic behavior of wild-caught females for male calling song at the time when parasitoid flies are most active. *Gryllus rubens* exhibits a wing dimorphism: males and females are either long-winged and capable of flight or short-winged and flightless. Both morph types were used in this phonotactic experiment in the proportion that they were available. I used two methods of collecting crickets; some were collected by turning over objects and debris and others were captured using sound traps (Walker 1986). I used the two methods because I collected very few long-winged individuals by turning over objects and debris and sound traps captured long-winged individuals exclusively. All collections were made at the University of Florida Organic Garden, Alachua Co., FL.

Females were weighed to the nearest 0.001 g and housed individually in square plastic containers measuring 13 x 13 x 9 cm (l x w x h) with wire screen

lids. Each container had an inch of sand, an inverted egg carton shelter, and Purina Cat Chow and water ad lib. All containers were held under ambient light and temperature in a greenhouse less than 1 km from the collection site. After 10 days (the number of days necessary to ensure that the crickets were not parasitized by *O. ochracea*), I brought females to the lab and tested their preference for male calling song. Parasitized females were not used in these experiments. The actual sample size for the fall was $N_{long\text{-}winged}=24$ and $N_{short\text{-}winged}=16$. The sample size for the spring was $N_{long\text{-}winged}=23$ and $N_{short\text{-}winged}=17$.

Phonotactic tests were conducted in a rectangular arena (Fig. 3-1) measuring 1.0 x 0.3 x 0.3 m (l x w x h). The floor of the arena was made of compressed foam, and the walls consisted of metal 2 mm mesh wire screen . To prevent the crickets from climbing out of the arena, I taped a 5 cm wide paper strip along the wire screen walls 15 cm from the floor. On the outside at each end of the arena, I placed a Radio Shack model 277-1008 mini-audio amplifier speaker. These speakers were connected to a Sony model D-EJ721 portable CD-Walkman. Prior to a test, a female was placed in the center of the arena under an inverted egg carton shelter. I covered this shelter with a plastic cup and allowed the female to acclimate for 5 min. After that time, I lifted the plastic cup with a string attached to it and gave the female 5 min to choose between a silent speaker and a speaker broadcasting a male calling song. Output of the broadcasting speaker was set at 72dB, 15 cm in front of the speaker, using a Brüel & Kjær model 2219 sound level meter. This sound level falls within the

natural variation of sound intensities of calling males (M.J. Vélez, unpublished data).

I observed females in the arena using a 40 watt red light. Each female was tested only once two to three hours after sunset within the four-hour period when *O. ochracea* flies are most active (Chapter 2). For each test, I recorded the latency to leave the shelter, which end screen the female contacted first (criterion for female choice), and the time spent within 10 cm of the broadcasting speaker. The floor of the arena was lined with paper. Between tests, this paper was replaced, the metal wire screen walls were wiped with paper towels, and the position of the broadcasting speaker was randomized. No end biases were detected. I examined female phonotactic behavior in the laboratory from 12 June to 5 July (N=40) and 10 October to 6 December 2001 (N=40) because these are the times of year when flies are rare and abundant, respectively (Walker 1986). The temperature in these tests did not differ between the two times of the year ($Mean_{fall} \pm SE = 22.58 \pm 0.06$ °C, $Mean_{spring} \pm SE = 22.66 \pm 0.05$ °C, P=0.463).

This phonotactic experiment was conducted in the absence of *O. ochracea* flies because I assumed that females do not detect flies directly. I based this assumption on the finding that male crickets in the presence of flies do not sing differently than solitary males (S.M. Bertram, unpublished data).

I analyzed the time that females spent within 10 cm of the broadcasting speaker using a general linear model with model: season (fall, spring), collection method (turning over objects and debris, sound traps), morph (long-winged, short-winged), mass, season*collection method, season*morph, season*mass.

The P-value reported for each variable is the value after all other variables were taken into account. Data were analyzed using SPSS 11.5. Results are presented as means ± standard error.

Source of Male Calls

Male *G. rubens* produce a trilling song in which sound pulses are repeated and grouped into long pulse trains (Fig.3-2; Doherty & Callos 1991). Field-collected males were individually recorded in the lab using an Optimus model CTR-115 sound-activated cassette tape recorder. Ten males were recorded in the fall and 10 males in the spring. Each male was recorded for at least five minutes. The recordings of each male were digitized and divided to make four one-minute calls. This generated 40 fall calls and 40 spring calls. The digitized 1-min calls were bumed onto CD discs, and one of these calls was played back repeatedly to each female for 5 min during the preference test. Each female received a different call. Fall females were tested with fall calls and spring females with spring calls. The temperature at which males were recorded did not differ between the fall and the spring ($Mean_{fall}$ ± SE = 21.88±1.33 °C, $Mean_{spring}$ ± SE = 22.75±0.80 °C, P=0.584). This temperature also did not differ from the temperature during the female phonotactic tests ($Mean_{rec}$± SE = 22.31±0.76 °C, $Mean_{phon}$ ± SE = 22.63±0.04°C, P=0.684).

Fly Activity

To verify that *O. ochracea* flies are more active in the early evening in the fall but not the spring, I monitored fly activity in a pasture at the University of Florida Beef Teaching Unit, Alachua Co., FL. To monitor fly activity, I used a slit trap (Walker 1989) with an electronic sound synthesizer that broadcasts calls of *G. rubens* (4763 Hz carrier frequency, 50.0 pulses per second, 50% duty cycle; continuous trill at 80 dB, 15 cm above the speaker). I activated the synthesizer an hour before sunset and counted the number of flies captured at the trap 4 h later. I carried out this procedure from 5 June to 12 July (N=20) and from 10 October to 26 November 2001 (N=20) because these were the times when females were tested in the phonotactic experiment.

Results

Phonotactic Experiment

Fewer females chose the broadcasting speaker in the fall (20/40; 50%), than in the spring (30/40; 75%) (Fisher's exact test: P=0.013). Fall females also spent less time within 10 cm of the broadcasting speaker (Fig. 3-3; ANOVA, season, $F_{1,72}$=9.736, P=0.003) than spring females. Furthermore, fall females took longer to leave the shelter than spring females (Fig. 3-4; t-test: N_{fall}=40, N_{spring}=40, t=3.115, P=0.003). In general, upon leaving the shelter, fall females tended to walk around it and after some time, many of them went to the endscreen with the silent speaker and walked around that area. In contrast, spring females tended to leave the shelter and walk directly to the endscreen

with the broadcasting speaker. Many of them climbed the metal screen wall facing the speaker walking back and forth in front of the broadcasting speaker.

The time that females spent within 10 cm of the broadcasting speaker was not significantly affected by collection method (ANOVA, collection method, $F_{1,72}$=0.227, P=0.635) or morph type (ANOVA, morph, $F_{1,72}$=0.009, P=0.926). Similarly, the time that females spent within 10 cm of the broadcasting speaker was not significantly affected by the interaction between season and collection method (ANOVA, season*collection method, $F_{1,72}$=0.208, P=0.650) or the interaction between season and morph (ANOVA, season*morph, $F_{1,72}$=0.124, P=0.726).

Female mass had a significant effect on the time that females spent within 10 cm of the broadcasting speaker (ANOVA, mass, $F_{1,72}$=5.231, P=0.025). This effect differed between the seasons. In the spring the time that females spent within 10 cm of the broadcasting speaker decreased with female mass but not in the fall (Fig. 3-5, ANOVA, season*mass, $F_{1,72}$=8.219, P=0.005).

Fly Activity

More flies were captured in the early evening per night in the fall than in the spring ($Mean_{fall}$ ± SE = 2.6±0.8, $Mean_{spring}$ ± SE = 0.2±0.1, Mann-Whitney U test, U=317, n_{fall}=20, n_{spring}=20, P<0.001).

Discussion

This study demonstrates seasonal changes in female *G. rubens* phonotactic behavior to male calling song. Parasitoid flies are most abundant in the fall and most active in the early evening (Chapter 2). In the spring, flies are rare. Because females may be parasitized as they approach singing males, I predicted that fall females should be less phonotactic to male calling song in the early evening than spring females. The results of this study support this prediction. Fewer females chose the speaker that was broadcasting male calls in the fall than in the spring, and fall females spent less time near the broadcasting speaker than spring females. These results are consistent with the hypothesis that risk of parasitism decreases female attraction to males with sexually-selected traits.

Few studies have examined the effect of risk on female choice for sexually selected traits. French and Cade (1987) examined female mating behavior in *G. texensis* housed in large outdoor arenas. This field cricket is also parasitized by *O. ochracea* (Cade 1975). Their results showed that females mated more frequently around dawn, which coincided with the time when parasitoid flies were less active (Cade et al. 1996). Similarly, Hedrick and Hill (1993) examined female preference for long-bout calls in *G. integer* in the presence and absence of cover. In this species, females prefer long-bout calls over short bout calls (Hedrick 1986) all else being equal. However, when females were given a choice between a long-bout call played across open space and a short-bout call played through 100% cover, females did not express a preference for long-bout calls, suggesting

that the increased predation risk associated with open space reduced the attractiveness of long-bout calls. Similar results have also been found in sand gobies and guppies (Forsgren 1992, Godin & Briggs 1996). Typically, females of these two species prefer to mate with brightly colored males. However, this preference disappeared when females had to choose in the presence of a predator. Collectively, these results are consistent with the findings of this study and support the hypothesis that when choice is risky, the intensity of sexual selection declines.

In this study, females were collected using two methods; turning over objects and debris, and using sound traps. The use of sound traps may have introduced a bias since individuals that were captured using this method were initially attracted to male calling songs. However, this possibility was not supported because collection method and the interaction between season and collection method did not have significant effects on the time that females spent within 10 cm of the broadcasting speaker. Another bias that may have affected the results of this study is that different numbers of long- and short-winged females were collected in the fall and spring. However, again, this was not supported because morph type and the interaction between season and morph type did not significantly affect the time that females spent within 10 cm of the broadcasting speaker. Collectively, these results suggest that seasonal changes in female phonotactic behavior were not due to seasonal changes in the effects of collection method or morph type.

The time that females spent near the broadcasting speaker decreased with female mass in the spring but not the fall (Fig. 3-5). This seasonal difference in the interaction between female mass and phonotactic behavior may be due to seasonal differences in the mating experience of females. Female crickets mate multiply (reviewed by Loher & Dambach 1989). Their mating experience has been shown to affect their phonotactic behavior. Lickman et al. (1998) presented females differing in mating experience with multi-stimulus songs. Their results show that virgin females exhibited more directional movement towards male songs than mated females. Virgin females may be more phonotactic than mated females since this will increase the chances that they will mate at least once and secure some sperm. In this study, if heavy females in the spring were old and mated, and light females were young and virgin, then this relationship may explain why female phonotaxis decreased with female mass in the spring. This is possible because *G. rubens* has two pulses of adults in the fall and spring, and two smaller cohorts of adults in the summer and winter (T.J. Walker, unpublished data). At the time that spring females were collected from the field (15 May to 25 July 2001), the summer cohort was starting to emerge as adults. Therefore, I could have collected both mated spring females, and virgin summer females. In contrast, because at the time that fall females were collected (1 October to 25 November 2001), no females from the winter cohort had yet emerged. This would mean that my fall sample may have primarily consisted of mated fall females. This could explain why phonotactic behavior did not decrease with female mass in the fall. It is important to note, however, that even when this

seasonal interaction between female phonotactic behavior and female mass is taken into account, season still has a significant effect on female phonotactic behavior.

Fall females took longer to leave the shelter during the phonotactic experiment than spring females. This seasonal difference in female behavior may be interpreted as fall females behaving more cautiously around male calls than spring females in order to reduce fly parasitism or other sources of increased risk. This explanation is consistent with a study on *G. integer* in which males differing in song conspicuousness were presented with a novel, potentially dangerous predator stimulus (Hedrick 2000). Males with more conspicuous songs took longer to emerge from a shelter after the predator stimulus than males with less conspicuous songs. Hedrick (2000) interpreted these differences in latency to leave the shelter as males compensating behaviorally for their conspicuous mating displays. This interpretation is consistent with the findings of this study for females and suggests that future work should examine how parasitism risk affects female searching behavior.

Fall females took longer to leave the shelter than spring females. Could this difference in behavior account for the shorter time that females spent within 10 cm of the broadcasting speaker in the fall than in the spring? This is possible because time spent in the shelter is time that could not have been spent near the broadcasting speaker. However, some evidence suggests that this is unlikely. The mean time that fall females spent in the shelter was 98 sec (Fig. 3-4). This means that fall females spent on average 202 sec outside of the shelter. This

time is much greater than the mean time that spring females spent within 10 cm of the broadcasting speaker, 121 sec (Fig. 3-3). These results suggest that seasonal differences in female latency to leave the shelter do not fully explain the seasonal variation in the time that females spent within 10 cm of the broadcasting speaker.

This study has important implications for understanding the evolution of sexually-selected traits. Male *G. rubens* sing to attract females for mating. This behavior, however, also attracts parasitoid flies in some populations, in some seasons, and at some times of the night. Differences in male calling behavior between populations, seasons, or time of the night have been interpreted as due to the natural selection pressure, parasitism. However, if parasitism risk also decreases female attraction to male calls, then males may derive fewer benefits from calling. In this study, I have found that fall females are less attracted to male calling song in the early evening than spring females. This reduction in the strength of sexual selection, as well as the increased natural selection costs for males, will weaken selection for calling in the early evening for fall but not spring males. Therefore, fall and spring males should differ in the timing of calling behavior. Fall males should not sing in the early evening, but spring males should sing at that time. This prediction has been confirmed in *G. rubens* (Chapter 2): surveys of calling males in the field showed that fewer males sing in the early evening in the fall than in the spring. This correlation between female behavior and male calling behavior suggests that future studies investigating variation in sexually selected traits should examine not only how risk affects

natural selection on males with sexually selected traits, but also how risk affects female choice for males with sexually selected traits, and hence the benefits of conspicuous traits.

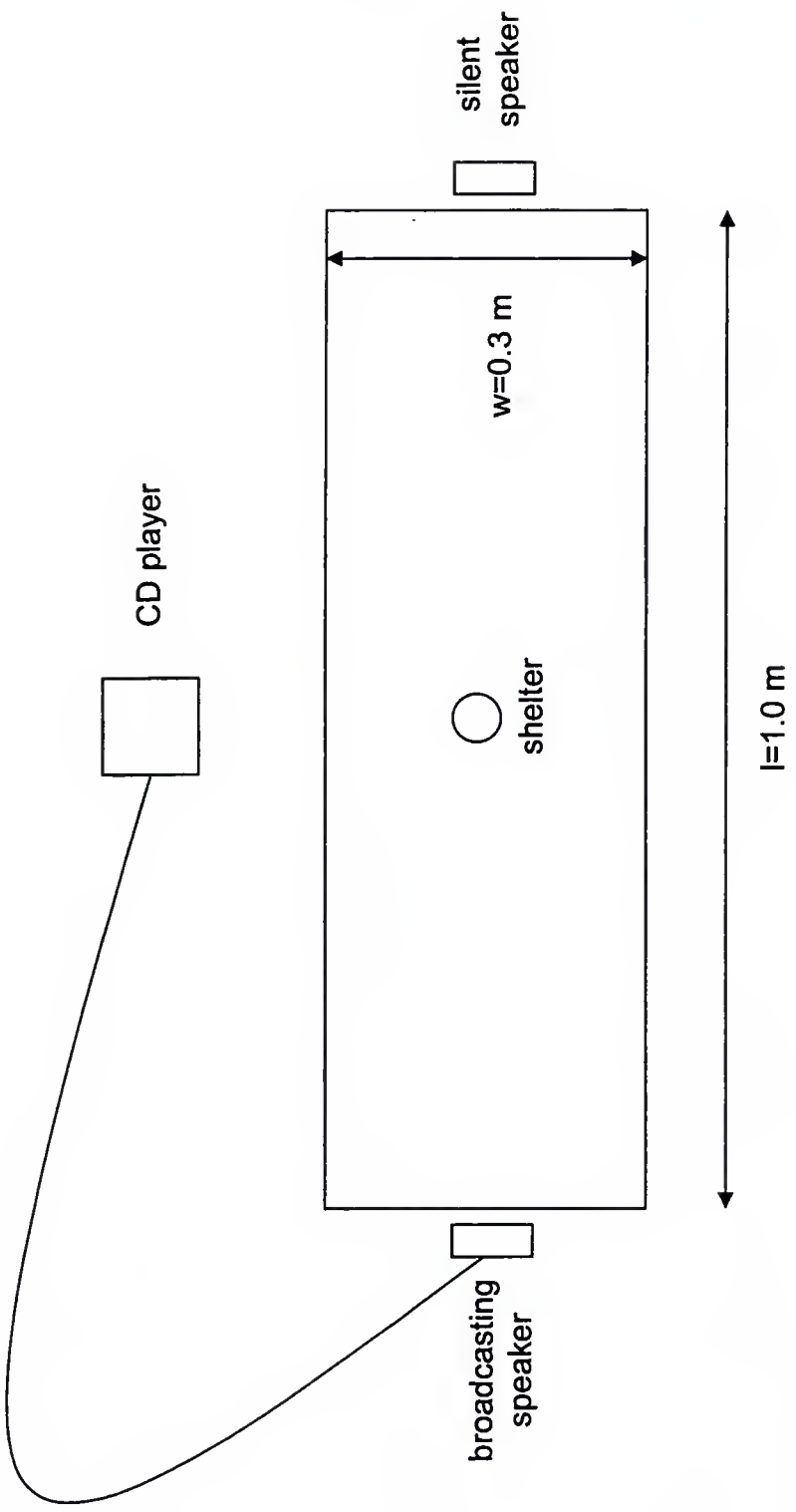

Fig. 3-1. Experimental arena used in phonotactic experiment.

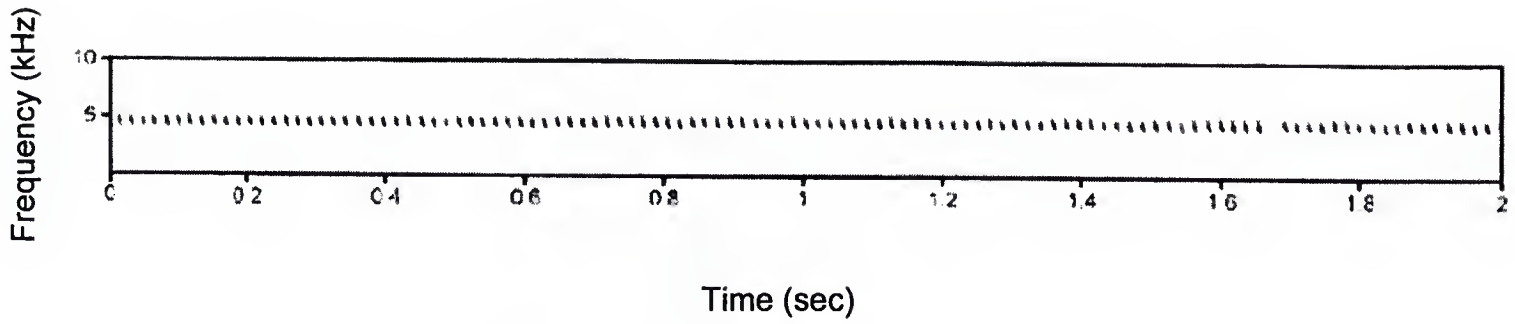

Fig. 3-2. Sound spectrograph of *Gryllus rubens* calling song at 25.4°C (SINA).

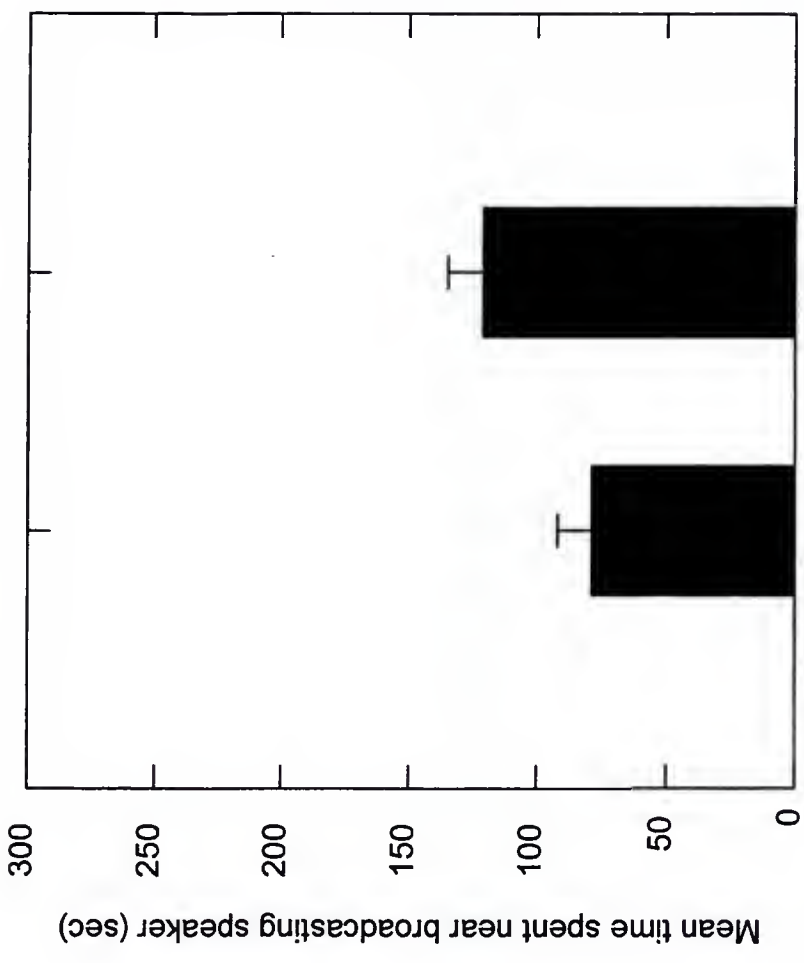

Fig. 3-3. Seasonal differences in the mean time spent by female *Gryllus rubens* within 10 cm of a broadcasting speaker in a phonotactic experiment where fall (N=40) and spring (N=40) females chose between a silent speaker and a speaker broadcasting a male calling song.

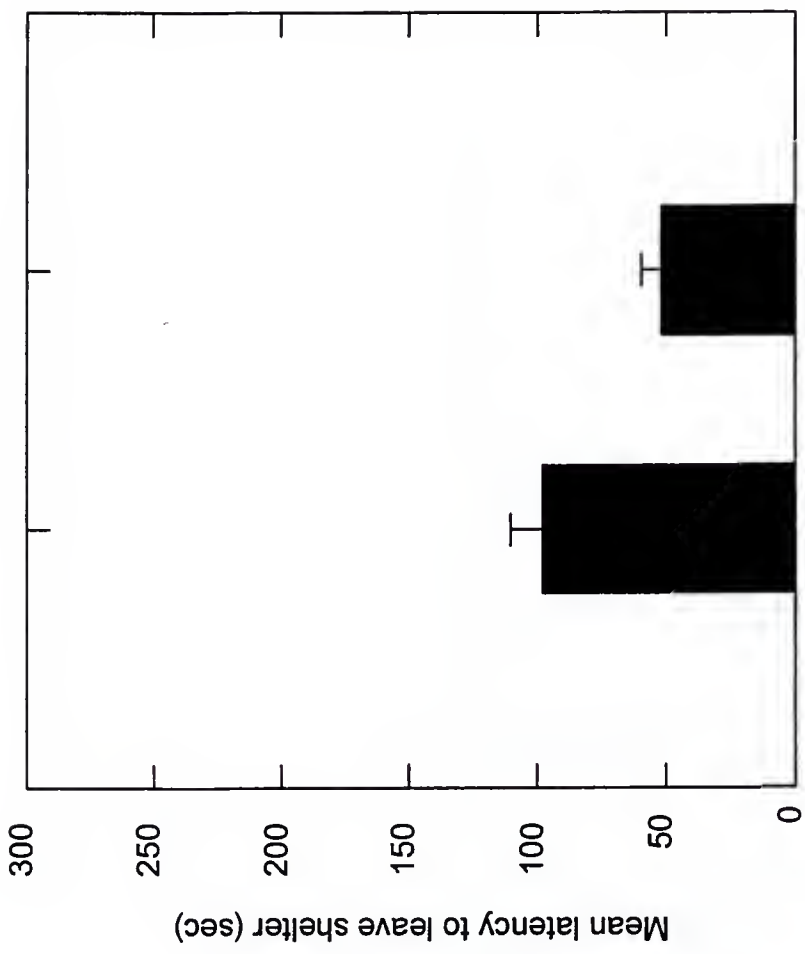

Fig. 3-4. Seasonal differences in the mean latency to leave the shelter by female *Gryllus rubens* in a phonotactic experiment where fall (N=40) and spring (N=40) females chose between a silent speaker and a speaker broadcasting a male calling song.

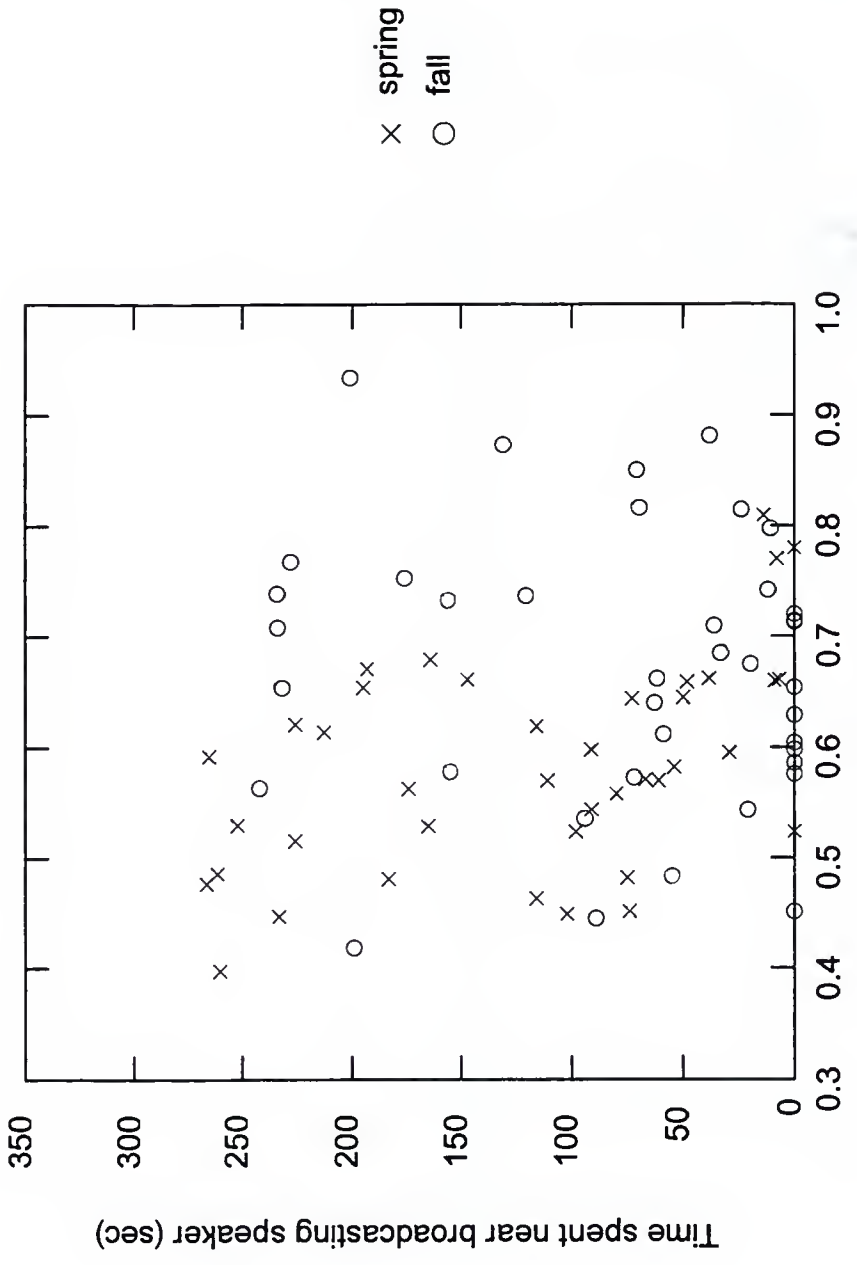

Fig. 3-5. Seasonal differences in the association between female *Gryllus rubens* mass and time spent by females within 10 cm of a broadcasting speaker in a phonotactic experiment where fall (N=40) and spring (N=40) females chose between a silent speaker and a speaker broadcasting a male calling song.

CHAPTER 4
VARIATION IN SEXUAL SELECTION FOR MALE SONG IN THE FIELD CRICKET *GRYLLUS RUBENS*

Introduction

A primary goal of sexual selection theory is to understand how natural and sexual selection interact to favor variation in male sexually-selected traits (Andersson 1994). Crickets represent an ideal system in which to study this question for several reasons. First, calling song is highly variable among males (for review see Bertram 2002). Such variation can be easily quantified by individually recording males and digitally analyzing their songs. Second, male song attracts conspecific females for mating. Typically, females approach singing males and mount them (Loher & Dambach 1989). This suggests that male calling is affected by sexual selection. Finally, male vocalizations also attract parasitoid flies (Cade 1975, Walker 1986, 1993). Female flies deposit larvae on and around calling males, killing infected crickets within 7-10 days (Walker 1986, 1993). This means that male calling may also be affected by natural selection. Collectively, these conditions make crickets an ideal system to study how natural and sexual selection interact to favor variation in male sexually-selected traits.

One of the most variable song characters in male crickets is nightly calling duration or the total time spent calling per night. Using an artificial selection experiment, Cade (1981) demonstrated that much of the variation in nightly calling duration in the cricket, *Gryllus texensis*, was due to genetic differences

among males. Subsequently, Cade and Wyatt (1984) found that nightly calling duration was highly variable among male *G. texensis*, *G. pennsylvanicus*, *G. veletis*, and *Teleogryllus africanus*. Similarly, Cade (1991) determined that nightly calling duration was also highly variable among male *G. integer* and *G. rubens*. Despite the potential role of sexual selection in explaining variation in male cricket song, most studies examining variation in nightly calling duration have ignored the effect of sexual selection (Cade 1984, Cade & Wyatt 1984, French & Cade 1989, Sakaluk & Snedden 1990, Forrest et al. 1991, Cade & Cade 1992, Gray 1997, Wagner & Hoback 1999, Kolluru et al. 2002, but see Bertram 2002). The goal of this study is to examine whether seasonal variation in male *G. rubens* nightly calling duration is correlated with seasonal variation in sexual selection.

In northern Florida, male *G. rubens* that sing spend more time calling in the fall than in the spring (Chapter 2). Three factors have been used to explain variation in male cricket calling behavior: male condition, parasites, and density. Nightly calling duration should increase with male condition because males in good condition are better able to bear the energetic costs of calling than males in poor condition (Sakaluk & Snedden 1990, Forrest et al. 1991, Gray 1997, Wagner & Hoback 1999). However, this possibility is not supported by the available data for *G. rubens*. Although fall males are heavier than spring males, nightly calling duration does not increase with male mass (Chapter 2). Similarly, parasitized males should call less than unparasitized males because parasites decrease the ability of males to sing (Cade 1984, Kolluru et al. 2002). However,

this hypothesis does not explain seasonal variation in *G. rubens* calling since unparasitized fall and spring males differed in nightly calling duration (Chapter 2). Finally, males at high densities should sing less than males at low densities because as density increases, the costs of defending territories increase as well as the chances of encountering a female by searching without calling (Alexander 1961 & 1975, Otte 1977, Cade 1979, Cade & Wyatt 1984, French & Cade 1989, Cade & Cade 1992). But, differences in density cannot explain the longer calling duration of fall *G. rubens* because male densities are higher in the fall than in the spring (Veazey et al. 1976). Taken together, it is unlikely that the three most common explanations can account for the seasonal changes in male *G. rubens* nightly calling duration.

The same male *G. rubens* vocalizations that attract females also attract gravid females of the parasitoid fly *Ormia ochracea* (Walker 1986, 1993). These females deposit larvae on and around calling males, killing infected crickets within 7-10 days. If parasitoid flies attack males more in the spring than in the fall, then this seasonal difference in parasitism risk may explain the seasonal differences in nightly calling duration. However, for *G. rubens* this is not an explanation because *O. ochracea* in northern Florida is abundant in the fall and rare in the spring (Walker 1986, Chapter 2) and fly parasitism rates are higher in the fall than in the spring (10% versus 0%, Walker & Wineriter 1991). Therefore, seasonal changes in parasitism risk cannot explain the seasonal changes in male *G. rubens* calling duration.

Males that sing may have longer calling durations in the fall than in the spring because seasonal changes in photoperiod and temperature cause fall and spring males to differ in nightly calling duration. This possibility is supported by rearing studies showing that photoperiod and temperature may affect calling song parameters. Walker (2000) reared male *G. rubens* under different photoperiods and temperatures to examine whether developmental conditions affect pulse rate. He found that temperature influenced pulse rate, but photoperiod did not. Similarly, Olvido and Mousseau (1995) reared striped ground crickets (*Allonemobius fasciatus*) under two environments differing in photoperiod and temperature. Their results showed that chirp rate, chirp duration, interchip interval, pulse number, and carrier frequency are affected by rearing environments. Despite this work, no study has ever found a significant effect of photoperiod on male nightly calling duration in crickets. Bertram and Bellani (2002) reared male *G. texensis* under fall-like and spring-like photoperiods and found that rearing photoperiod does not significantly affect nightly calling duration in males. This suggests that seasonal differences in male *G. rubens* nightly calling duration are not due to seasonal changes in photoperiod. However, the effect of temperature during development on nightly calling duration has not been tested in any cricket species.

Male *G. rubens* may exhibit seasonal changes in nightly calling duration if the benefits of singing change seasonally. These benefits may vary seasonally if sexual selection operates differently in the two seasons. Accordingly, I hypothesized that males sing longer in the fall than in the spring because the

benefit of singing increases with calling duration in the fall but not in the spring. I evaluated this hypothesis by using pitfall traps fitted with speakers broadcasting male calling songs of different duration. I counted the number of females captured at the traps in the fall and spring. and predicted that the number of captured females should increase with calling duration in the fall but not in the spring. This prediction is important because it would be the first evidence to suggest seasonal variation in sexual selection. Such variation could favor variation in the sexually-selected trait, male calling duration.

Methods

Pitfall Trap Experiment

I examined seasonal variation in sexual selection for nightly calling duration from 14 April to 12 June and 23 September to 5 November, 2002 because these are times when males sing for short and long durations, respectively (Chapter 2). During both fall and spring, female and male *G. rubens* occur in two forms, long- and short- winged. The two morphs differ in their ability to fly as well as in other life-history characteristics such as the onset of reproduction (Roff 1984, Zera & Rankin 1989, Holtmeier & Zera 1993). Females of both morphs were used in this study in the proportions in which they occurred. All experiments were conducted in a field at the University of Florida Environmental Landscape Horticulture Education Lab, Alachua Co., FL. I chose this field because male *G. rubens* sing all year long at this site.

Tests for seasonal variation in sexual selection for nightly calling duration were conducted using five pitfall traps (Fig. 4-1) laid out in a straight line 10 m apart. Each trap was made by excavating a hole in the ground and placing a 2.4 L plastic bucket measuring 17 x 15 cm (height x diameter) in the hole so that the rim was level with the ground. Over each bucket I placed a plastic funnel 10 cm tall with an upper diameter of 18 cm and a spout diameter of 6 cm. The funnel rested on the rim of the bucket and the spout was 7 cm above the bottom of the bucket. I placed a 33-cm square PVC tube frame (1.9 cm diameter) with four 7-cm legs over the bucket-funnel trap. The frame rested on the ground surrounding the bucket-funnel trap and supported a metal grill top with 1.5 cm spaces between the bars. In the center of this grill top, I positioned a Sony model D-EJ721 portable CD-Walkman with a Radio Shack model 277-1008 mini-audio amplifier speaker lying flat over the CD player. The speaker pointed upward and rested 9 cm over the center of the trap. Crickets that were attracted to calls played on the CD player, flew (long-winged morph) or walked (short-winged morph) into the bucket-funnel trap where they were collected hourly. Five different treatments of male calling duration were used, one for each pitfall trap. The treatments consisted of broadcasting male calling songs for 0, 1, 2, 3, or 4 hours. These calling durations fall within the natural variation of time spent calling by males (Chapter 2). Output of the broadcasting speakers was set at 80dB, measured 15 cm above each speaker, using a Brüel & Kjær model 2219 sound level meter. This sound level falls within the natural range of sound intensities of calling males (M.J. Vélez, unpublished data).

Each experiment began an hour before sunset when I activated the CD player over the pitfall trap set to broadcast for 4 h. An hour later, I turned on the CD player over the pitfall trap set to broadcast for 3 h. This continued until all CD players broadcasting songs had been activated. The outcome of this staggering the onset of the calling was that all CD players finished broadcasting male calling songs three hours after sunset. This pattern was used because individual recordings of males under field conditions show that calling start times are inversely related to calling duration (M.J. Vélez, unpublished data). The pitfall trap with the 0-h treatment was handled like the pitfall trap set to broadcast for 4 h: a CD player was placed over the trap an hour before sunset. However, this player did not broadcast any songs. This treatment controlled for the number of non-phonotactic females that fell into a trap. All pitfall traps were checked hourly to count the number of captured females from one hour after the experiment started to the end of the experiment three hours later. Trapped females were removed from the field to ensure that they were not sampled in more than one treatment or night. Any trapped males or juveniles were released back into the field. Each night constituted one replicate of the experiment. All treatments within a replicate used the same male calling song, but different replicates used different songs. Between replicates, I randomized the position of the treatments. Randomization was achieved by generating all possible combinations of treatments and picking one at random each night. This experiment was conducted on 35 nights in the spring and 25 nights in the fall.

Source of Male Calls

Male *G. rubens* were collected from the field using sound traps (Walker 1986). They were housed individually in square plastic containers measuring 13 x 13 x 9 cm (l x w x h) with wire screen lids. Each container had an inch of sand, a few pieces of Purina Cat Chow (changed daily) and water ad lib. All containers were held under ambient light and temperature in a greenhouse less than 1 km from the collection site. After 10 days (the number of days necessary to ensure that the crickets were not parasitized by *O. ochracea*), I brought the males into the lab and individually recorded each for at least 5 min using an Optimus model CTR-115 sound-activated cassette tape recorder. All of the males used in these recordings were unparasitized and long-winged because short-winged males could not fly into the sound traps used to collect crickets. Ten males were recorded in the fall and 10 males in the spring. The recordings of each male were digitized and used to make four 1 min calling songs. This generated 40 fall and 40 spring calling songs. These songs were burned onto CD discs and played back repeatedly in the pitfall trap experiment for the duration of the treatment. In the fall, I used fall calling songs over pitfall traps, and in the spring, I used spring calling songs. The mean temperature at which males were recorded was 23.1°C and did not differ between fall and spring calls (t-test, P=0.702).

Data Analysis

A generalized linear model with a Poisson distribution and a logit link was used to regress the calling duration of a treatment on the number of females

captured in that treatment's pitfall trap. This model was used because the data could not be transformed to achieve normality. Because treatments within a replicate were not statistically independent, I used a mixed model to analyze the data. In this model, calling duration was a fixed effect, and replicate number was a random effect. Fall and spring data were analyzed separately. The data were tested for overdispersion to validate the use of the Poisson model.

If females search for mates at different times of the night in the fall and spring, then such seasonal differences in female behavior could affect the relationship between calling duration and number of trapped females. To evaluate this possibility, I compared the capture time to the nearest hour of each female in the pitfall traps during the fall and spring using a Mann-Whitney U test.

Data were analyzed using R 1.7.1 (Dalgaard 2002) and Systat 6.0 (Wilkinson 1997). Descriptive results are presented as means ± standard error.

Results

The number of captured females increased with treatment calling duration in the fall but not in the spring (Table 4-1; Fig. 4-2; fall: $t=4.532$, $df=99$, $P<0.001$; spring: $t=0.419$, $df=139$, $P=0.676$). Females were captured in all calling duration treatments in the spring and fall with the exception of the 0-h treatment in which no female was captured in either the fall or the spring (Fig. 4-2). Sixteen females arrived at the pitfall traps in the fall ($n_{long}=12$, $n_{short}=4$), and 10 in the spring ($n_{long}=6$, $n_{short}=4$). Fall and spring females did not differ in the time at which they were captured in the pitfall traps (Fig. 4-3; $n_{fall}=16$, $n_{spring}=10$, Mann-Whitney U

test=56.5, P=0.189). This non-significant result remains even when the number of females captured in the first two hours are compared with the number of females captured in the last two hours in the fall and spring (X^2=0.005, df=1, P=0.940)

Discussion

Male *G. rubens* that sing spend more time calling in the fall than in the spring (Chapter 2). This is surprising because there are more phonotactic, parasitoid flies present in the fall (Walker 1986, Chapter 2) so one would expect males to call less to avoid parasitism. Furthermore, as I argued in Chapter 3, females should be less attracted to calling males in the fall because they too are parasitized by these flies (Walker & Wineriter 1991). The results of the pitfall trap study provide an explanation: males that sing longer are more likely to attract females during the fall but not during the spring (Table 4-1). What might explain this result?

If fall females search for mates in the early evening and spring females search for mates in the late evening, then these temporal differences in female activity may explain why the number of captured females in my pitfall traps increased with calling duration in the fall but not the spring. This is possible because of the way I set up the experiment: the long calling duration treatments began earlier in the evening than the short calling duration treatments. Consequently, fall females, preferring to search for mates in the early evening, would have a higher probability of encountering a pitfall trap with a long calling

duration whereas spring females, preferring to search for mates in the late evening, would have an equal probability of encountering a long or short calling duration treatment. However, the results of this study do not support this explanation. Fall and spring females did not differ in the time at which they were captured in the pitfall traps. This suggests that male calling duration increases in the fall but not the spring because long duration calls are more effective at attracting females in the fall but not in the spring. This pattern is consistent with seasonal variation in sexual selection.

Female *G. rubens* densities in northern Florida are higher in the fall than in the spring (Veazey al. 1976). If females choose males randomly with respect to calling duration, then males with long duration calls should have a higher probability of attracting females than males with short duration calls. Because this probability should increase proportionally with density, seasonal changes in female density cannot explain the seasonal changes in the success of long duration calls. Instead, the seasonal differences in the success of long duration calls suggest that fall females do not have a preference for calling duration and spring females prefer short duration calls. Theoretical models on the evolution of female preferences show that choosiness decreases when the risks of choice increase relative to the benefits (Parker 1983, Kirkpatrick 1987, Pomiankowski 1987, Real 1990, Iwasa et al. 1991). Parasitoid flies are abundant in the fall and rare in the spring (Walker 1986, Chapter 2). Fall females may not have a preference for calling duration because the costs of choice due to fly parasitism may be high in that season. Even though females do not sing, they are

nonetheless parasitized to the same levels as males are (Walker & Wineriter 1991). In contrast, females are more phonotactic in the spring than in the fall (Chapter 3). In an experiment giving females a choice between a silent speaker and a speaker broadcasting a male calling song, fewer females chose the speaker that was broadcasting male calls in the fall than in the spring, and fall females spent less time near the broadcasting speaker than spring females. This may mean that less singing is required to attract females in the spring than in the fall. This seasonal variation in sexual selection is consistent with the seasonal changes in the success of long duration calls.

The results of this study are consistent with recent work showing within- and between-population variation in the female preference functions of field crickets. Wagner et al. (1995) sequentially presented female *G. integer* from a single population with songs differing in the number of pulses per trill, inter-trill interval, or the proportion of missing pulses within a trill. These presentations revealed that individual females differed significantly in their preference functions based on the number of pulses per trill and inter-trill interval. Furthermore, these preference functions were highly repeatable within females. Similarly, Simmons et al. (2001) examined geographic variation in the female preference function for the long chirp portion of male *Teleogryllus oceanicus* calling song. Their results show that the female preference function for the amount of long chirps differed between populations. The findings from these studies suggest that selection can act on female preference functions. The outcome of such process may favor variation in male sexually-selected traits.

To evaluate the general importance of temporal variation in sexual selection as a mechanism favoring variation in male sexually-selected traits, future studies should examine how variation in female choice is affected by factors that change the costs and benefits of choice, such as predation, parasitism, sex ratios, and population densities. If any of these factors fluctuates in time, then the costs and benefits of choice as well as the resulting female choice patterns may also vary temporally. In turn, this temporal variation in female choice could act to favor variation in sexually-selected traits

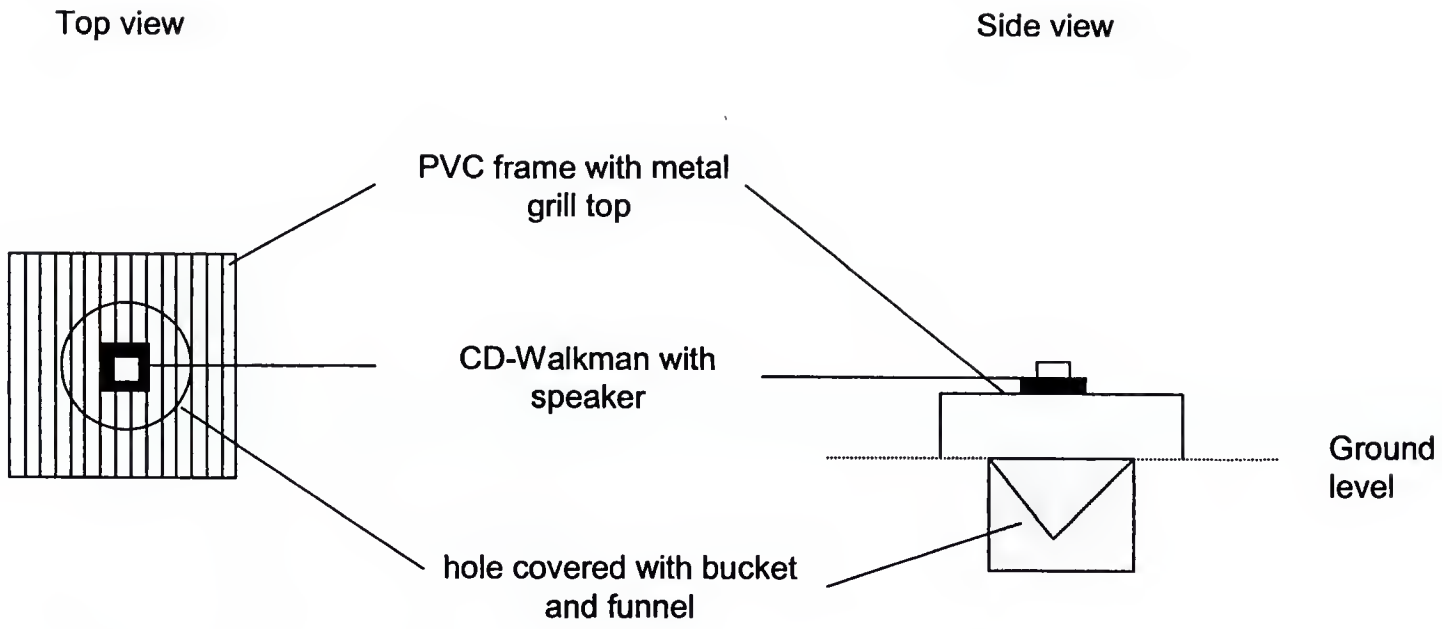

Fig. 4-1. Pitfall trap used to test *Gryllus rubens* female choice for male calling duration. Each trap was made by excavating a hole in the ground. This hole was deep enough to accommodate a 2.4 L bucket measuring 17 x 15 cm (height x diameter). The rim of the bucket was level with the ground. The bucket was covered with a large plastic funnel 10 cm tall that rested on the rim of the bucket, spout down. The funnel had an upper diameter of 18 cm and a spout diameter of 6 cm. A square PVC frame (length = 33 cm) with four 7-cm legs was positioned over the funnel and bucket. This frame rested on the ground surrounding the bucket-funnel trap. The frame supported a metal grill top. A CD-Walkman with an external speaker facing upward rested on the metal grill top. The speaker was positioned 9 cm over the center of the trap.

Table 4-1. The effect of season on male *Gryllus rubens* nightly calling duration. The table shows the results of a generalized linear model with a Poisson distribution used to regress treatment calling duration on the number of captured females in that treatment's pitfall trap. Because treatments within a replicate were not statistically independent, a mixed model was used to analyze the data. In this model, calling duration was a fixed effect, and replicate number was a random effect. Each season was analyzed separately.

Season	Parameter	Value	Std. Error	DF*	t-Value	P-value
Fall	Intercept	-4.238	0.577	99	-7.342	< 0.001
	Slope	0.716	0.158	99	4.532	< 0.001
Spring	Intercept	-3.073	0.625	139	-4.916	< 0.001
	Slope	0.100	0.239	139	0.419	0.676

* Degrees of freedom were calculated with the formula: #nights (# treatments – 1) – 1.

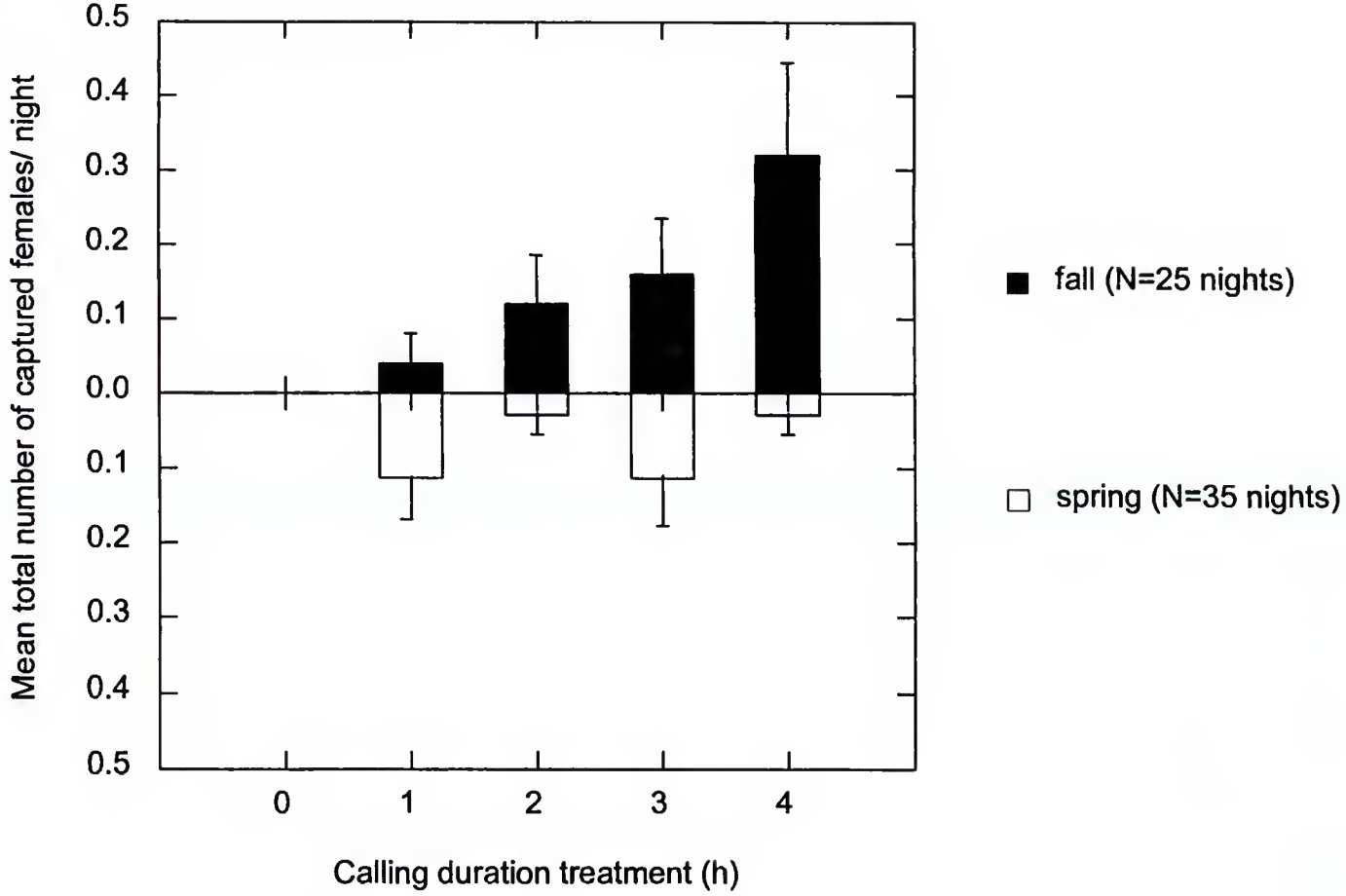

Fig. 4-2. Seasonal differences in the mean total number of female *Gryllus rubens* captured in the pitfall trap experiment. Five treatments were presented in each replicate; each broadcasted male calling song for a different duration (0, 1, 2, 3, and 4 h). Each pitfall trap was checked hourly to count the number of captured females (which were then removed). Each night constituted one replicate of the experiment.

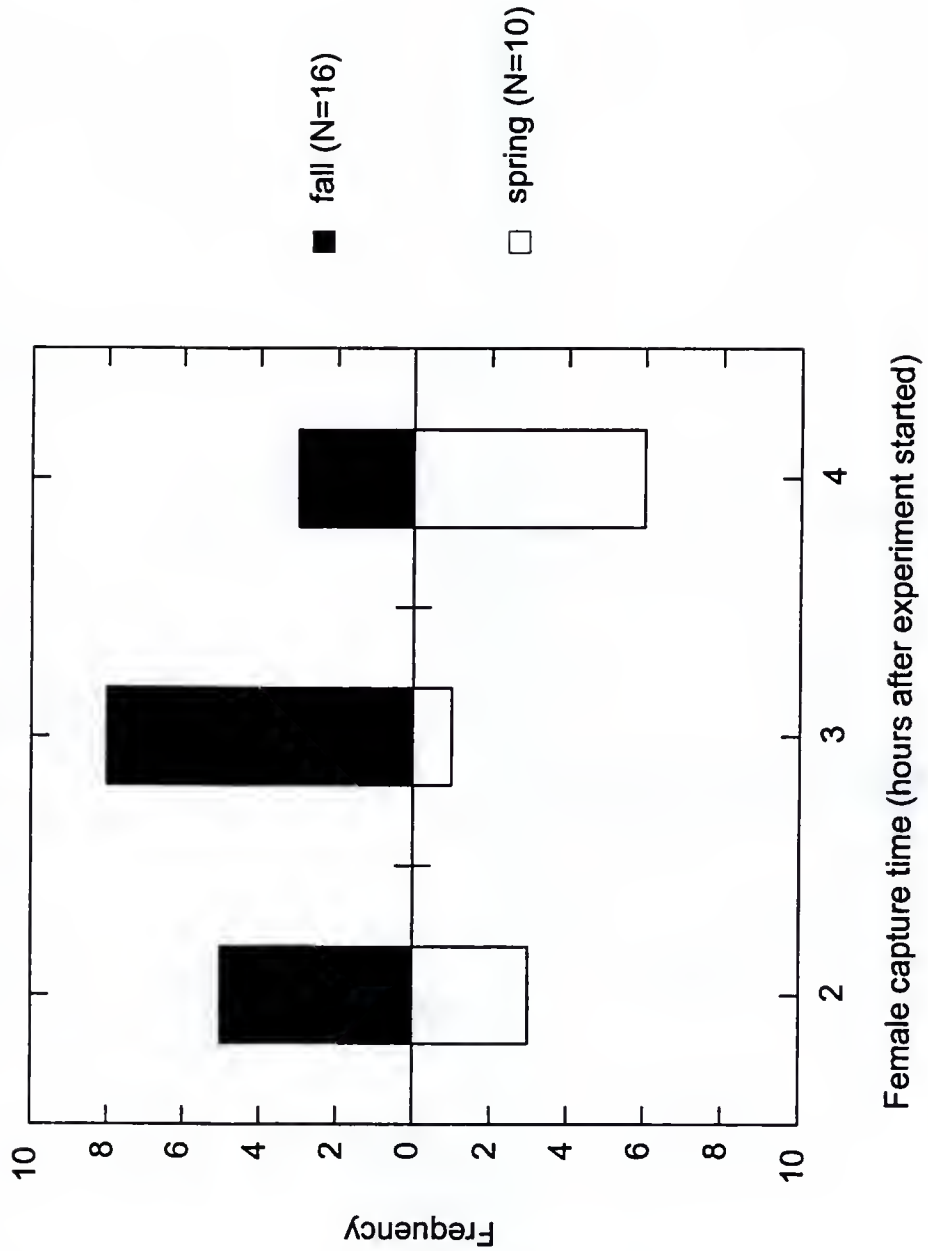

Fig. 4-3. Seasonal differences in female *Gryllus rubens* capture time in the pitfall trap experiment. In this experiment, five pitfall traps broadcasting male calling songs for 0, 1, 2, 3, and 4 h were checked hourly to estimate to the nearest hour the capture time of each female that fell into the trap.

CHAPTER 5
GENERAL MODEL: A TEST OF THE FACTORS AFFECTING MALE CALLING DURATION IN THE FIELD CRICKET *GRYLLUS RUBENS*

Factors Affecting Male Calling Duration

Fall and spring generations of the field cricket *Gryllus rubens* in northern Florida experience different selective pressures and social environments. Males of this species sing which attracts females for mating. Their calling song also attracts gravid females of the parasitoid fly *Ormia ochracea* (Walker 1986, 1993). These female flies deposit larvae on and around calling males, killing infected crickets within 7-10 days. In the fall when parasitoid flies are abundant (Walker 1986, Chapter 2), and cricket densities are high (Veazey al. 1976), calling songs of long duration attract more females than short duration calling songs (Table 4-1, Fig. 4-2). This is quite different from the spring when parasitoid flies are rare (Walker 1986, Chapter 2), cricket densities are low (Veazey al. 1976) and calling song duration does not affect female attraction rates (Table 4-1, Fig. 4-2). In this chapter, I examine how seasonal changes in fly parasitism, female visitation rates, and cricket density should alter the costs and benefits of calling for fall and spring males. I evaluate these effects by building a model that calculates the fitness of different calling durations in each season. I then use this model to predict observed seasonal patterns in calling duration. Additionally, I independently vary the effects of fly parasitism and female choice on male calling duration within each season to evaluate the relative importance of natural versus

sexual selection in favoring seasonal patterns in male calling duration. This model is valuable because it is the first to evaluate simultaneously the effects of fly parasitism, female attraction rates, and cricket density on the male character, calling duration. This model also provides insights into how different selective pressures and social environments can interact to favor variation in a male trait.

Model: Predicting Seasonal Patterns in Male Calling Duration

Male Calling Strategies

In this model, males can adopt one of four calling strategies: (1) call for 1 h, (2) call for 2 h, (3) call for 3 h, and (4) call for 4 h. These calling durations fall within the natural range of time spent calling by male *G. rubens* under field conditions (Fig. 2-4; Cade 1991). I assume that males adopt one calling strategy and use it throughout their lifetime. This assumption is supported by the finding that the mean time spent calling per 24 h under laboratory conditions does not change with male age in *G. texensis*, *G. pennsylvanicus*, *G. veletis*, and *Teleogryllus africanus* (Cade & Wyatt 1984). Furthermore, Cade (1981) found that some of differences between male *G. texensis* in calling duration are due to genetic differences among males.

Individual field recordings of male *G. rubens* show that some males do not call (Fig. 2-4). These males may obtain mates by walking around searching for females. This alternative male tactic has been documented in several species of field crickets (French & Cade 1989, Hissmann 1990, Zuk et al. 1993, Hack 1998). I did not include this behavior in my model because little is known about the

mating success and parasitism risk of walking males. Cade (1979) proposed that walking males may have decreased mating success on any given day, but they may have higher survival rates and longer lifespans than calling males because they do not attract as many parasitoid flies. This hypothesis, however, remains untested and hence I exclude non-calling as a strategy in my model.

Calculating Fitness of Male Calling Strategies

Male calling attracts conspecific females and parasitoid flies. Each calling strategy carries a mating benefit, M, and a probability of escaping fly parasitism, E. Each day, males mate before they face fly parasitism. The daily fitness of each calling strategy F_i is defined as:

$$F_i = E_iM_i + (1-E_i)M_i,$$

where i is the calling strategy.

If a male sings and is not parasitized on a given night, he accrues the mating benefit of that day and sings again in the next day. If a male sings and is parasitized on a given night, he accrues the mating benefit of that day. After fly parasitism, the infected male has one more day to carry out his calling strategy and receive the corresponding mating benefit. After that day, the infected male does not get any further reproduction. This restriction is meant to mimic the temporal dynamics of the effects of fly parasitism on male calling duration. Kolluru et al. (2002) experimentally infected male *T. oceanicus* with *O. ochracea* larvae and monitored the proportion of time spent calling by males each night after fly parasitism. Their results show that the proportion of time spent calling by

males remained unchanged the day after fly parasitism but declined sharply to almost zero after the second day.

I calculated the lifetime fitness of each calling strategy using the formula:

$$\sum_{d=1}^{d=60} M_i(d+1)(1-E_i)E_i^{\,d-1}$$

where d equals day and the length of the breeding season is 60 days. This formula individually adds the daily fitness of each strategy over the 60 days of the breeding season for all possible outcomes (i.e., male is parasitized on the first day, male avoids fly parasitism on the first day and is parasitized on the second day, male avoids fly parasitism on the first and second day and is parasitized on the third day, etc.). Fitness was calculated using R 1.7.1 (Dalgaard 2002).

Seasonal Changes in Mating Benefit (M)

Long duration calling songs are more likely to attract females than short duration calling songs in the fall but not the spring (Table 4-1; Fig. 4-2). This seasonal pattern in female attraction suggests that the mating benefit of singing should increase with calling duration in the fall but not the spring. I estimated the mating benefit of the different calling strategies in each season using data from a field experiment carried out in the fall and spring in which I counted the number of females captured at pitfall traps fitted with speakers broadcasting male calling songs differing in duration (1 h, 2 h, 3 h, and 4 h; Fig. 4-2). Because the number of captured females increased with calling duration treatment in the fall, I used the mean number of captured females per night for each treatment to estimate

the mating benefit of each calling strategy in the fall (Table 5-1). Because there was no significant relationship between calling duration treatment and number of captured females in the spring, I assumed that all calling strategies have a similar mating benefit in the spring. I estimated this mating benefit by calculating the mean number of captured females per night for all calling treatments combined (Table 5-1). These seasonal changes in mating benefit with calling duration indicate that males that call more attract more females in the fall but not in the spring.

Female density may also affect the mating benefit of the different calling strategies. Males should call less at high densities because females may be easier to locate without calling and calling territories may be more expensive to defend at high than at low densities (Alexander 1961 & 1975, Otte 1977, Cade 1979). Because cricket densities are higher in the fall than in the spring, males should call less in the fall than in the spring. This potential seasonal effect of density on the mating benefit of the different calling strategies is already taken into account in the empirical estimates of seasonal changes in mating benefit due to differences in female visitation rates. This is because the pitfall traps used to collect these data captured females at their natural densities in each season.

Seasonal Changes in Probability of Escaping Fly Parasitism (E)

Calling males attract parasitoid flies (Cade 1975). Walker and Wineriter (1991) experimentally muted *G. rubens* males by removing the right tegmen. They found that muted males have lower fly parasitism rates (0/10) than unmuted

males (7/13) under field conditions at high fly densities. This finding suggests that the probability of escaping fly parasitism should decrease with calling duration. To estimate this relationship more precisely, I used data collected in the fall on the arrival times of flies captured at a slit trap broadcasting male *G. rubens* calling song (Chapter 2). The number of flies arriving at the trap decayed rapidly with time (Fig. 2-1). These data can be used to estimate the probability of escaping fly parasitism for different calling strategies because male calling start times are inversely related to calling duration. To achieve this, I fitted a negative exponential equation to the data on fly arrival times using a generalized mixed linear model with a Poisson distribution. I used this equation to estimate the probability of at least one fly infecting a male of each calling strategy. To accomplish this, I used data collected in the fall on the probability of at least one fly arriving at a slit trap broadcasting male *G. rubens* calling song for 4 h (Chapter 2). I set this probability as the y-intercept in the negative exponential equation I derived earlier and used this equation to calculate the probability of at least one fly infecting a male that sings for 1 h, 2 h, and 3 h. The outcome of these manipulations is that the probability of escaping fly parasitism decreased with calling duration in the fall (Table 5-1). This relationship between the probability of escaping fly parasitism and calling duration indicates that males that call more have lower survival rates and shorter lifespans than males that call less. This is because the cumulative probability of escaping fly parasitism in this model decreases more rapidly for long calling durations than for short calling durations

over the 60 days of the breeding season. The end result is that this model incorporates the tradeoff between calling duration and life span for fall males.

Walker (1986) estimated that fly abundance in the spring is 1% of the fly abundance in the fall. This means that the probability of escaping fly parasitism should be higher for all calling strategies in this season. I estimated this probability for each strategy by increasing their counterpart fall probability by 99%. This assumes that there are 99% fewer flies in the fall than in the spring, fly parasitism risk increases linearly with parasitoid fly abundance, and the probability of escaping fly parasitism decreases with calling duration in the same way as it does in the fall (Table 5-1).

Model Results: Seasonal Changes in Fitness of Male Calling Strategies

The fitness of calling strategies increased with calling duration in the fall but not the spring (Fig. 5-1). In the fall, the strategy 'call 4 h' had the highest fitness, and 'call 1 h' had the lowest fitness (Fig. 5-1). In the spring, the strategies 'call 1 h' and 'call 2 h' had the highest fitness, and 'call 3 h' and 'call 4 h' had the lowest fitness (Fig. 5-1).

Comparison of Optimal Seasonal Strategies with Observed Calling Durations

Even though parasitoid flies are more common in the fall than in the spring (Walker 1986, Chapter 2), male *G. rubens* spent more time calling in the fall than in the spring (Fig. 2-5). This finding agrees with the predictions of my model. The fitness of calling strategies increased with calling duration in the fall but not the

spring. The probability of escaping fly parasitism decreased with calling duration in both the fall and spring. In the fall, however, this increased cost of singing with calling duration was offset by a disproportionate increase in the mating benefit with calling duration. This resulted in calling strategies with long calling durations obtaining higher fitness than calling strategies with short calling durations. In contrast, the increased cost of singing with calling duration in the spring was not offset by the mating benefit because this benefit did not change with calling duration. This resulted in calling strategies with short calling durations achieving higher fitness than calling strategies with long calling durations.

A comparison of the mean calling duration of male *G. rubens* in the fall and spring with the optimal seasonal calling durations predicted by my model reveals that males sang about as much as expected in the spring (0.71 h vs. 1 or 2 h) and less than expected (1.71 h vs. 4 h) in the fall. One possible explanation for this discrepancy is that my model did not include the energetic costs of calling. Such costs are known to increase linearly with calling duration in trilling species of crickets like *G. rubens* (Prestwich & Walker 1981). Fall males may have not sung as much as predicted because it may be more costly to sing in the fall than in the spring. This could occur if temperatures are higher in the fall than in the spring. It is clear that if these seasonal changes in the energetic costs of calling were incorporated into my model, then the predicted calling durations would be lower than the current ones in the fall.

Variations of the Model

To evaluate the relative importance of natural versus sexual selection in favoring seasonal patterns in male calling duration, I independently varied the effects of fly parasitism and female visitation rates on male calling duration within each season. In the first variation of the model, I drastically reduced fly parasitism by setting the probability of escaping fly parasitism to 0.999 for all calling strategies in the fall and spring (Table 5-2). I then examined the fitness of the different calling strategies given only seasonal variation in the mating benefit (Table 5-2). This would be the situation, for example, in a population with few flies, which may be found in the northern extent of the *G. rubens* range. In the second variation of the model, I held the mating benefit constant for all calling strategies in the fall and spring by assigning all strategies the average mating benefit for both seasons combined (Table 5-3). I then evaluated the fitness of the different calling strategies given only seasonal variation in the probability of escaping fly parasitism (Table 5-3). This would simulate the effect of a population in which there was no relationship between calling duration and female visitation rates.

Results of Model Variations

In the model with reduced and constant fly parasitism, and variable mating benefit, the results are the same as when fly parasitism was included: the fitness of longer duration calling strategies increased in the fall but not the spring (Fig. 5-2). In the fall, the calling strategy 'call 4 h' had the highest fitness, and the

strategy 'call 1 h' had the lowest fitness (Fig. 5-2). In the spring, all calling strategies had the same fitness (Fig. 5-2). In the model with variable fly parasitism and constant mating benefit (Fig. 5-3), however, the results are not the same as when mating benefit varied: the fitness of calling strategies 'call 1 h' and 'call 2 h' were higher than the fitness of strategies 'call 3 h' and 'call 4 h' in both the fall and the spring

Relative Importance of Natural versus Sexual Selection

Reducing fly parasitism and holding it constant did not affect the general pattern of the original model: the fitness of longer calling duration strategies increased with calling duration in the fall but not the spring in both models. This finding suggests that sexual selection may be more important than natural selection in favoring seasonal patterns in male calling duration. Male *G. rubens* calling durations may have been higher in the fall than in the spring because long duration calls were more effective at attracting females in the fall than in the spring. This implication is significant because it suggests that variation in sexual selection may be more important than variation in natural selection in shaping the evolution of male traits.

Even though sexual selection may be more important than natural selection, nonetheless sexual selection and natural selection clearly interact to shape seasonal patterns in male *G. rubens* calling duration. In the model with variable fly parasitism and constant mating benefit, short calling strategies had

higher fitness than long calling strategies. This suggests that natural selection can modulate the effects of sexual selection on male calling duration.

Implications of the Model

The conclusions of this model enhance our understanding of how natural and sexual selection may interact to favor variation in sexually selected male traits. In *G. rubens*, male song attracts both females and parasitoid flies. Signals that attract both mates and predators or parasites are common in species where males have sexually selected traits (for review see Burk 1982). The outcomes of my model show that in systems like this one, sexual selection may be more important than natural selection in favoring variation in male traits, but that natural selection can modify the effects of sexual selection.

Seasonal variation in calling duration has been observed in other *Gryllus* species. Male *G. texensis* sing to attract females for mating and their calling song also attracts *O. ochracea* (Cade 1975). The risk of fly parasitism in male *G. texensis* may increase with calling duration because the number of *O. ochracea* flies attracted to broadcasts of *G. texensis* song increases with calling duration (Cade et al. 1996). Because *O. ochracea* is more abundant in the fall than in the spring, the risk of fly parasitism should be higher in the fall than in the spring. Cade (1989) studied female *G. texensis* attracted to male calling song in late summer and early fall. He found that the number of females attracted to male song increased with calling duration. Unfortunately, Cade (1989) did not examine female *G. texensis* attraction to male song in the spring. However, if female *G.*

texensis attraction to male song does not increase with calling duration in the spring, as in the closely related species *G. rubens*, then *G. texensis* would be similar to *G. rubens* in the seasonal changes in mating benefit and probability of escaping fly parasitism. Accordingly, my model would predict that male *G. texensis* should spend more time calling in the fall than in the spring. Bertram (2002) found evidence for this prediction, although she had a different explanation for the cause. This finding supports the general conclusions of this model in explaining seasonal variation in male *G. rubens* calling duration.

This model is valuable because its formulation is general enough to explain variation in any sexually selected male trait that attracts both females and predators or parasites. Such tradeoffs in sexually selected traits are well known (Burk 1982; Godin & Briggs 1996). For example, this model could be used to evaluate geographical variation in male color patterns of guppies (*Poecilia reticulata*). Male guppies show extensive geographical variation in their conspicuous color patterns. Their bright colors are preferred by females (Kodric-Brown 1985, Houde 1987, Long & Houde 1989) but at the same time make the males more vulnerable to predation (Endler 1987). This variation has been explained by a balance between female preference for conspicuous males and natural selection against conspicuous males (Endler 1983). However, studies over the last two decades have shown that female preferences also vary with predation levels (Breden & Stoner 1987, Stoner & Breden 1988, Godin & Briggs 1996; Brooks & Endler 2001). Female preference for conspicuous males disappears when predation is high. This means that the geographical variation in

male guppy color patterns may be due to differences among populations in sexual selection as well as natural selection (Dill et al. 1999).

My model could help examine the relative importance of natural versus sexual selection in favoring geographical patterns of male color patterns in species like guppies. The strategies of the model could be different areas of conspicuous body colors or different levels of bright coloration. The mating benefit of the different color areas could be estimated from studies examining female preference for male color patterns in low and high predation areas. Similarly, the probability of escaping predation in geographic areas with different color strategies could be estimated from studies examining the survival of males under low and high predation levels. Once these parameters are calculated, they could be manipulated using my model to assess the relative importance of natural versus sexual selection in favoring geographical variation in male guppy color patterns. If the gain in fitness through sexual selection (female preference) shows an accelerating effect whereas natural selection (risk of predation) is linear with color brightness, then the results will be similar to my model with *Gryllus*: the effect of sexual selection has a stronger effect on driving variation in male color variation than natural selection. This application shows how my model could be used to examine variation in any sexually selected male trait that attracts both females and predators.

Table 5-1. Model Variables: Mating benefit and probability of escaping fly parasitism of different male *Gryllus rubens* calling strategies in the fall and spring.

Male Calling Strategy	Mating Benefit (mean # females attracted/ night)		Probability of Escaping Fly Parasitism/ night	
	Fall	Spring	Fall	Spring
Call 1 h	0.040	0.070	0.500	0.995
Call 2h	0.120	0.070	0.500	0.995
Call 3h	0.160	0.070	0.350	0.697
Call 4h	0.320	0.070	0.350	0.697

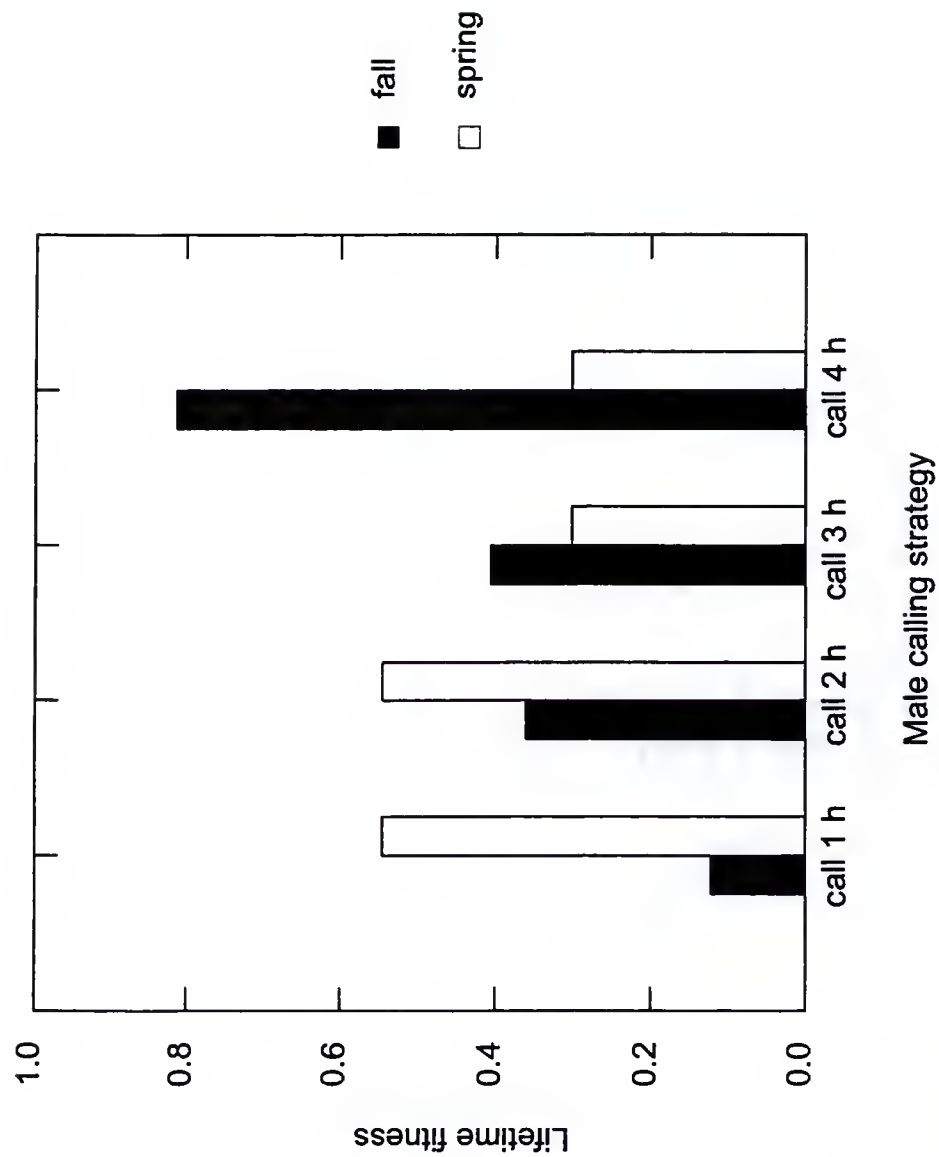

Fig. 5-1. Model Results: Seasonal changes in the lifetime fitness of different male *Gryllus rubens* calling strategies.

Table 5-2. Model variables with reduced and constant fly parasitism and variable mating benefit. The table shows the mating benefit and probability of escaping fly parasitism of different male *Gryllus rubens* calling strategies in the fall and spring.

Male Calling Strategy	Mating Benefit (mean # females attracted/ night)		Probability of Escaping Fly Parasitism/ night	
	Fall	Spring	Fall	Spring
Call 1 h	0.040	0.070	0.999	0.999
Call 2h	0.120	0.070	0.999	0.999
Call 3h	0.160	0.070	0.999	0.999
Call 4h	0.320	0.070	0.999	0.999

Table 5-3. Mating benefit and probability of escaping fly parasitism of different male *Gryllus rubens* calling strategies in the fall and spring for model with variable fly parasitism and constant mating benefit.

Male Calling Strategy	Mating Benefit (mean # females attracted/ night)		Probability of Escaping Fly Parasitism/ night	
	Fall	Spring	Fall	Spring
Call 1 h	0.120	0.120	0.500	0.995
Call 2h	0.120	0.120	0.500	0.995
Call 3h	0.120	0.120	0.350	0.697
Call 4h	0.120	0.120	0.350	0.697

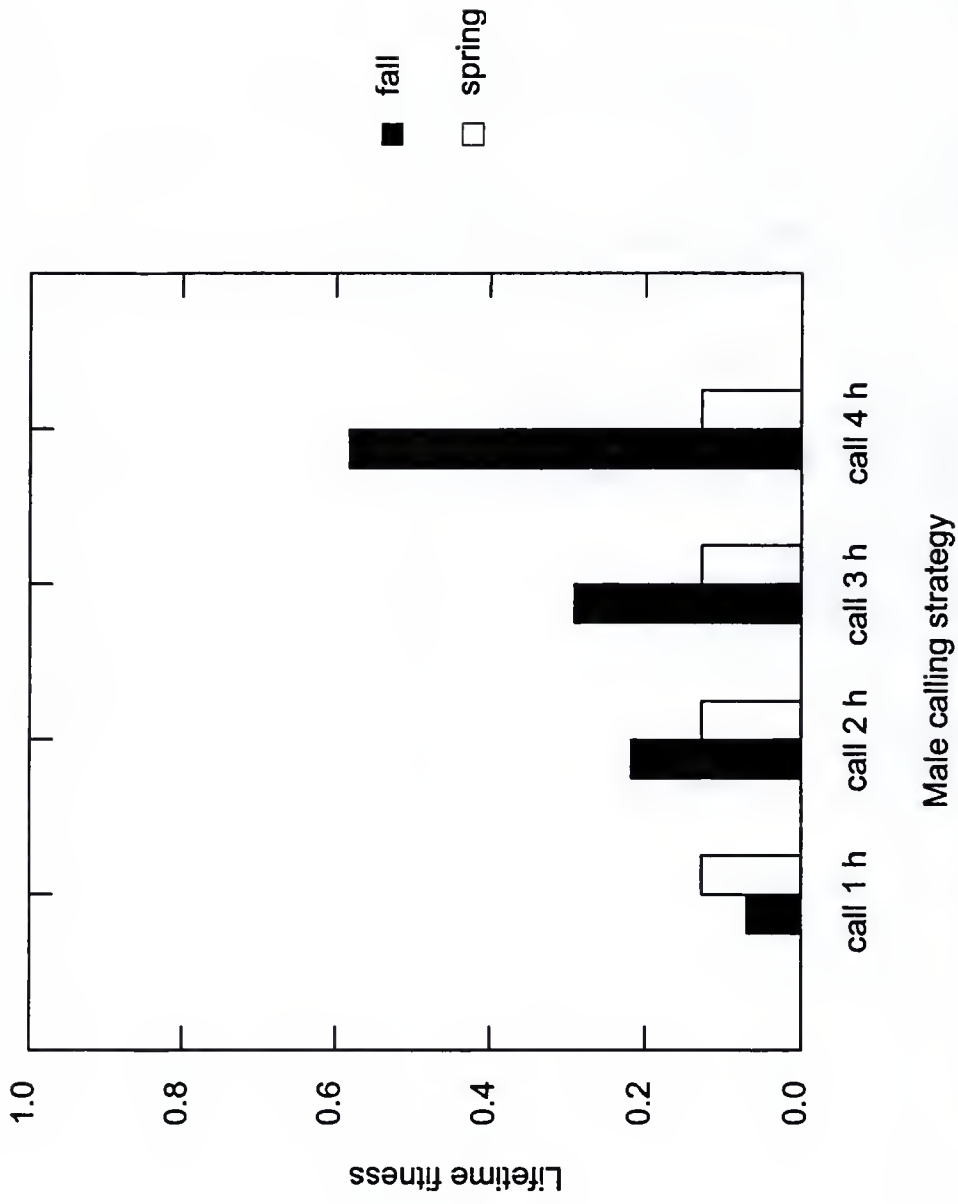

Fig. 5-2. Seasonal changes in the lifetime fitness of different male *Gryllus rubens* calling strategies in model with reduced and constant fly parasitism, and variable mating benefit.

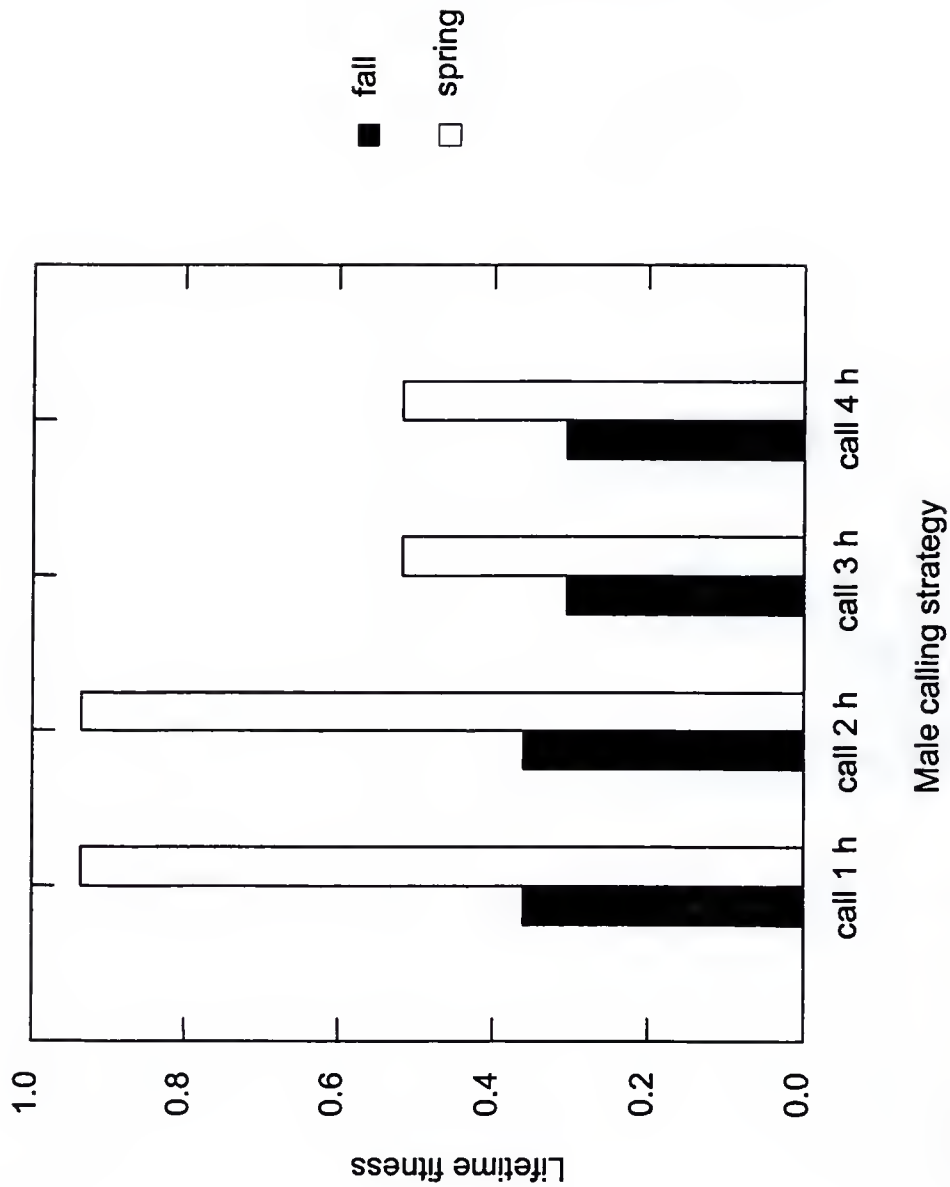

Fig. 5-3. Model Results with variable fly parasitism risk and constant mating benefit. The figure shows seasonal changes in the lifetime fitness of different male *Gryllus rubens* calling strategies.

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BIOGRAPHICAL SKETCH

Manuel J. Vélez was born in San Juan, Puerto Rico, on February 4, 1974. He is the son of Manuel J. Vélez Jr., a college professor of invertebrate zoology at the University of Puerto Rico, and Alsacia Bosch de Vélez, a social worker and housewife. He grew up in San Juan, where he attended elementary school at Colegio Nuestra Señora de la Providencia, and middle and high school at Colegio San Ignacio de Loyola. After graduating from high school, he left San Juan and attended Cornell University, where he earned a B.A. in biology with a concentration in neurobiology and behavior. While at Cornell University, he conducted behavioral research both in the field and lab in a wide range of taxa including fish, birds, and mammals. After graduating from Cornell University, he attended the University of Florida, where he earned an M.S. degree in zoology. His master's thesis explored parental care strategies in the cichlid fish *Aequidens coeruleopunctatus*. After he obtains his Ph.D. in zoology, he will attend Boston University School of Law, where he will study intellectual property.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

H. Jane Brockmann, Chair
Professor of Zoology

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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